ASSESSING THE IMPACTS OF INTENSIVE FOREST PRACTICES ON BIODIVERSITY IN FRAGMENTED LANDSCAPES IN PORTUGAL

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ABSTRACT

The Mediterranean basin is a biodiversity hotspot which is being threatened by land abandonment and afforestation, most notably with eucalypt plantations, but little research has been done to assess their impact. This study evaluated the impact of eucalypt plantations on biodiversity in the Mediterranean area, taking Portugal as a case study and amphibians, bats and carnivores as the target groups.

The impact of eucalypt cover and other landscape, stand and local variables was evaluated in relation to: species richness and species occurrence for amphibians, namely if amphibian species occurrence is influenced by local characteristics (micro-scale), land-use cover (migration and dispersion-scale) or a mix of both and whether the effects differ if the main cover is eucalypt plantations or *montado*; species richness, bat activity, Kuhl's bat *Pipistrellus kuhlii* (the most abundant bat species in the area) activity, for bats; and species occupancy and detection and spatial and temporal co-occurrence patterns for carnivores.

Amphibian species occurrence was, generally, not influenced by eucalypt cover, with the exception of the newt *Lissotriton boscai*, which was negatively affected, and *Salamandra salamandra*, which was positively affected. Overall, eucalypt plantations had a negative impact on bat activity, species richness and *Pipistrellus kuhlii* activity and negatively influenced carnivore detection probability across all species in both single and co-occurrence models. Eucalypt plantations had a negative effect on red fox (*Vulpes vulpes*) occupancy, whilst stone marten (*Martes foina*) and badger (*Meles meles*) preferred native land covers. However, eucalypt plantations had no effect on the interactions within this carnivore community.

This study confirms the negative impact of eucalypt plantations on bats and carnivores and suggests forest management guidelines to improve biodiversity at the stand and landscape scale. Namely, at a local scale, the implementation of a pond network of different hydroperiods and the exclusion/removal of exotic fish and promotion of understorey vegetation on eucalypt stands; at a landscape scale, it is suggested a multi-functional landscape, promoting eucalypt plantations with diverse age stands and the maintenance/promotion of native and patchy habitats.

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AUTHOR'S DECLARATION

The sampling survey was jointly designed by Dr. Miguel A. Carretero (Chapter 2), Dr. Hugo Rebelo (Chapter 3) and Dr. Pedro Sarmento (Chapter 4). The fieldwork for Chapter 2, Chapter 3 and Chapter 4 was carried out with the collaboration of Dr. Pedro Sarmento who also collaborated with the statistical analysis in Chapter 4. Gustaf Rydevik collaborated in the statistical analysis in Chapter 3. With those exceptions, I declare that the work contained in this thesis is my own and has not been submitted for any other degree or award.

Joana Cruz

CHAPTER 1

INTRODUCTION

1.1. Forest plantations

Forest plantations are "composed of trees established through planting and/or through deliberate seeding of native or introduced species" (FAO, 2010a). The concept and practice of forest plantations goes back to as early as 3000 BC, with the cultivation of olive trees (*Olea europaea*) in Greece (FAO, 2010b). Nowadays, global planted forest comprises 264 million hectares of which three quarters are grown for productive purposes (timber or non-wood forest products) with the remainder for protective purposes (FAO, 2010b). China, United States of America, India, the Russian Federation and Japan account for more than half of the worldwide forest plantation area – 53% (FAO, 2010a). Between 2000 and 2010 the global forest plantation area increased by 5 million ha per year (FAO, 2010a).

1.1.1 Effects of forest plantations on biodiversity

Considering these numbers, it is crucial to understand how plantations can make a positive contribution to biodiversity conservation and how potentially negative impacts of this land use can be minimised (Brockerhoff et al., 2009). There is a popular view that planted forests are "ecological deserts" (Gardner et al., 2007), but there is no consensus among researchers (Bremer & Farley, 2010). When comparing species richness and abundance between planted forests and primary forests, the overall conclusion is that the former is poorer (Bremer & Farley, 2010; Palacios et al., 2013; Pawar et al., 2004; Pineda & Halffter, 2004) (Table 1). That is not surprising due to the impact of silvicultural practices on soil properties, water retention, seed banks and understorey vegetation. Forest plantations may alter local and landscape characteristics and consequently change the micro-habitat, dispersal and seasonal migration conditions, prey availability, habitat use patterns or body condition (Table 1).

Table 1. Impacts of non-native forest plantations on the ecosystem (fauna and flora) when compared to natural forests. Equal signs indicate no difference; unequal signs mean difference; arrows represent direction of change (increase or decrease)

Country	Group	Impact on species				Reference
		Abundance	Diversity	Richness	Other	
China	Soil microbial community		↓	↓		Chen et al. (2013)
Spain	Epiphytic lichen	↓	↓			Calviño-Cancela et al. (2013)
South Africa	Riparian plants		↓	↓	↓ Structural attributes	Tererai et al. (2013)
Spain	Benthic macro-invertebrates				↓ Density	Martínez et al. (2013)
Mexico	Arthropods (Araneae)			↑		Corcuera et al. (2010)
Australia, Brazil, South Africa	Arthropods		↓	↓		Robson et al. (2009); Rocha et al. (2013); Samways et al. (1996)
Australia, Brazil, China, Madagascar, Malaysia, Puerto Rico (USA), Singapore, South Africa	Amphibians	↓	↓ and =	↓	= Density	Faruk et al. (2013); Fogarty and Vilella (2003); Gardner et al. (2007); Gillespie et al. (2012); Kudavidanage et al. (2012); Parris and Lindenmayer (2004); Rocha et al. (2013); Russell and Downs (2012); Sung et al. (2012); Vallan (2002)

Table 1. Cont

Country	Group	Impact on species				Reference
		Abundance	Diversity	Richness	Other	
Brazil, China	Reptiles	↓ and =	=	↓		Gardner et al. (2007); Rocha et al. (2013); Sung et al. (2012)
Brazil, China	Birds			↓		Marsden et al. (2001); Zou et al. (2014)
Malaysia	Mammals (Carnivora)				↑ Density	Mohamed et al. (2013)
Argentina	Mammals (Carnivora)				↓ Occupancy	Lantschner et al. (2012)
Chile	Mammals (Artiodactyla)				= Occupancy	Silva-Rodríguez and Sieving (2012)
Brazil	Mammals (Rodentia and Didelphimorphia)	↓		↓		Martin et al. (2012)

But there are exceptions to the rule. Disturbance-prone species may be favoured by forest plantations, although they may be of less conservation concern than other species (e.g. Faruk et al. (2013); Gillespie et al. (2012)). Pioneer species such as spiders belonging to the families Lycosidae, Oxyopidae and Salticidae, in Mexico, are more abundant in exotic eucalypt plantations than in native forests (Corcuera et al., 2010). Their ecological requirements - shallow leaf cover – are met in this kind of plantation, favouring their presence. Silvicultural practices such as clear-cut are ideal for ground foraging birds and open area species (Barbaro et al., 2009). If the plantation structure has more canopy gaps, the greater amount of light reaching the ground may promote dense and complex understorey vegetation. This usually leads to higher prey density than climax forests, whether it is arthropods (Zou et al., 2014) or rodents (Mohamed et al., 2013), and consequently greater predator diversity or abundance, as observed for understorey bird species (Zou et al., 2014) and leopard cat (*Prionailurus bengalensis*) density (Mohamed et al., 2013), for instance. Generalist heliothermic lizards, that favour open canopy, are more abundant in forest plantations than in native forests (Gardner et al., 2007). This decrease of one taxonomic component being compensated by the increase of another, usually one that is uncommon in native habitat, is called compensation categorical response (Sax et al., 2005).

Another type of response might be that there is no difference between natural forest and exotic plantation, and the value (e.g. species richness) of each taxonomic component in the different land covers is the same – an equivalency response (Sax et al., 2005). For example, reptile composition – all habitat generalists or open-area specialists species - was the same in secondary forest and exotic *Lophostemon confertus* plantations, due mainly to the long history of extirpation of native forests and consequent disappearance of forest specialists in the region long ago (Sung et al., 2012). The density of common coqui (*Eleutherodactylus coqui*) was similar in exotic eucalypt plantations and native forests, because both land uses provided complex understorey and midstorey which this species depends on (Fogarty & Vilella, 2003). Pudu (*Pudu puda*) occupancy, a globally vulnerable deer, is similar in the native forests and exotic eucalypt plantations of Chile, because both have a dense understorey, which provides refuge for the pudu (Silva-Rodríguez & Sieving, 2012). In New Zealand, mature exotic *Pinus radiata* plantations and native woodland have

similar composition of native beetle species (Pawson et al., 2008), but when considering also exotic beetle species, the conifer plantations have higher species richness than native forest, because the later is more resilient to colonization by non-native beetles.

Lastly, the original land cover or its present condition may play a significant part in understanding the impact of forest plantations. For instance, plant species richness in forest plantations is lower than in grassland, scrubland and primary forest, but higher than in degraded pastures (Bremer & Farley, 2010). There is evidence that tree plantations in degraded lands can promote the regeneration of plant diversity in the understorey, especially of shade-tolerant species, which can grow under the canopy (Coert, 1997; Loumeto & Huttel, 1997). Following certain prescribed measures, forest plantations may contribute to promote biodiversity in previously degraded land – greater use of native tree species, using species mixtures rather than monocultures or promoting diverse understorey vegetation are just a few examples (Lamb, 1998).

In summary, as a pattern, forest plantations have lower species richness, diversity and abundance than natural forests and this is even more evident when comparing exotic with native plantations (Table 1). However, generalist and open-habitat specialist species as well as pioneer species may in fact be favoured by forest plantations with their canopy gaps and simple composition. Other plantations, as a consequence of these canopy gaps, may develop dense and complex understorey vegetation which may provide prey that native climax forests lack and therefore create habitat to support a more diverse community. Finally, forest plantations can promote biodiversity in degraded sites if certain management and silvicultural practices are followed.

1.1.2 Effects of silvicultural practices on biodiversity

Many forest plantations are intensively managed, using improved tree varieties and silvicultural operations that include site preparation, thinning, clear-cut harvesting and short rotations (Brockerhoff et al., 2009). These practices and their impact on biodiversity have been thoroughly researched worldwide as exemplified below (see review in Fox (2000); Hayes et al. (2005)).

Mechanical site preparation

The primary goal of mechanical site preparation is to reduce competing vegetation and expose mineral soil (Moseley et al., 2004). But this management technique has often been associated with exposure of bare ground cover, reduction in soil depth, elimination of coarse-wood debris, decline in possible refuge sites (Moseley et al., 2004), and increase in soil temperature leading to high evaporation (Liao et al., 2011; Zhao et al., 2013). This simplification of the soil and ground cover affects the prey availability of many small vertebrates (Thompson et al., 2003). The impact of this action has led to decreased species richness and abundance (plants: Carneiro et al. (2008); Wen et al. (2010); amphibians: Morneault et al. (2004); reptiles: Enge and Marion (1986); birds: Hanberry et al. (2012)), and even a drastic decline of the frosted flatwoods salamander (*Ambystoma cingulatum*) in Florida, USA, when the land use was changed from savannah to slash pine (*Pinus elliottii*) plantations which interfered with its migration, breeding success, feeding and suitable refugia (Means et al., 1996).

Nevertheless, some types of mechanical site preparation have the potential to improve the soil conditions such as disking, bedding and subsoiling, as it increases the air and water transport through the soil (Morris & Lowery, 1988).

Thinning

Thinning is the selective process of removing trees to allow an optimum density that will permit the highest yield. It is a very-well studied practice and one that in most cases has a neutral or positive impact on biodiversity (insects: Maleque et al. (2010); Ohsawa (2004); birds: Hagar et al. (1996); Hayes et al. (2003); mammals: Barrett et al. (2012); Zwolak (2009)). But there are some species where abundance declined after thinning, including western red-backed salamanders (*Plethodon vehiculum*) (Grialou et al., 2000). These have been associated with direct machine impact and soil compaction. Thinning gives greater light access to ground cover favouring the development of complex understorey vegetation and additional cover sites, and promoting generalists and open-habitat species (Verschuyl et al., 2010). So, although a very common practice in the promotion of biodiversity in plantations, the responses to thinning are species-dependent and forest managers should also consider a matrix

with patches of differing tree densities to promote close-canopy species (Hayes et al., 2003; Patriquin & Barclay, 2003).

Clear-cut

Clear-cut can affect biodiversity by reducing canopy cover and availability of coarse-woody debris, exposing the animals to predators, soil compaction, and a reduction in water soil content by exposing the soil to high temperatures and increasing metabolic cost (Homyack et al., 2011) Examples in the literature of species richness and abundance declines after clear-cut are profuse (invertebrates: Pawson et al. (2011); amphibians: Popescu et al. (2012); Tilghman et al. (2012); mammals: Thornton et al. (2012)). The impact of clear-cut activities may extend beyond the clear-cut area to neighbouring habitats due to the edge-effect, which has been shown to be important in reducing abundance and species richness in both amphibians (Demaynadier & Hunter, 1998) and birds (Reino et al., 2009).

Removal of residual biomass

Another practice that has been reported to have had a negative impact on biodiversity is the removal of residual biomass after harvesting or thinning. This is a cost-effective procedure to obtain bioenergy material that reduces fire hazard in regions where the risk is particularly high (Pawson et al., 2013). However, this removal leads to lower deposition of coarse-wood debris essential for saproxylic invertebrates and cover for amphibians (Dahlberg et al., 2011; Otto et al., 2013) .

Short rotation

Most timber destined for pulpwood or biomass energy comes from short rotation plantations (< 10 years) (Pawson et al., 2013). This is a considerable advantage in a climate change scenario, because in a short period of time, an entire plantation could be replaced by different species or genotypes as well as adapting silvicultural practices to match climate alterations (Booth, 2013). However for biodiversity, the short rotation length and frequent disturbance may favour mainly early-successional species (Bremer & Farley, 2010) and limit the development of a complex understorey, both vertical and horizontal (Carnus et al., 2006). Forest associated with vascular plants showed low species richness in Sitka spruce (*Picea sitchensis*) and lodgepole pine (*Pinus contorta*) plantations managed for short rotations (35–45

years) (Coote et al., 2013). For forest bats, snags and older trees availability can be limited in short-rotation plantations, reducing the number of roosting sites (Hein et al., 2009; Hutson et al., 2001)

1.1.3 Use of exotic trees: the case-study of the eucalypt

The preference for the use of exotic trees in plantations is common worldwide. Prior to their use there is usually thorough research for selecting the most adequate species for each site in order to obtain optimum productivity, while reducing pest and disease problems. Of the several thousand tree species globally, only about 30 have been widely planted. Most of these are from just four genera, namely, *Acacia*, *Eucalyptus*, *Pinus* and *Populus* (Evans, 2009). *Eucalyptus globulus* was one of the first eucalypts to be used for plantations and by 1900 it could be found worldwide (Europe, Africa, Asia and South America) (Evans, 2009). Originally from Tasmania, at that time it was primarily planted for ornamental purposes or fuel wood. Nowadays it is largely used for pulpwood for which it is produced intensively, on a coppice rotation of about 10 to 16 years, usually twice or three times.

Worldwide, *Eucalyptus* species play an important role in pulp production, representing 8% of planted forests over 20 million hectares (Laclau et al., 2013). The fast growth rate and the low incidence of pests and diseases are the main characteristics that made the eucalypt one of the dominant trees for plantations (Turnbull, 1999). Introduced into more than 90 countries, only nine species and their hybrids dominate 90% of eucalypt plantations: *Eucalyptus camaldulensis*, *Eucalyptus grandis*, *Eucalyptus tereticornis*, *Eucalyptus globulus*, *Eucalyptus nitens*, *Eucalyptus urophylla*, *Eucalyptus saligna*, *Eucalyptus dunnii*, *Eucalyptus pellita* (Booth, 2013). Brazil, India and China have the highest area of eucalypt plantations in the world, with over 10 million hectares, and Portugal has the highest area in Europe (Iglesias Trabado & Wilstermann, 2008) (Fig. 1).

Eucalypt plantations are highly controversial and so are the impacts they have on the ecosystem, including effects on soil water and nutrients, erosion and biodiversity (Turnbull, 1999; Vacca et al., 2000). Eucalypt plantations in India are linked with reductions on soil depth and soil water retention and content, decrease of nutrient and

organic matter in one case (Bargali et al., 1993) but no more than the native *Tectona grandis* plantations in another case (Calder et al., 1993) or other native hardwoods when comparing evapotranspiration (Cannell, 1999).

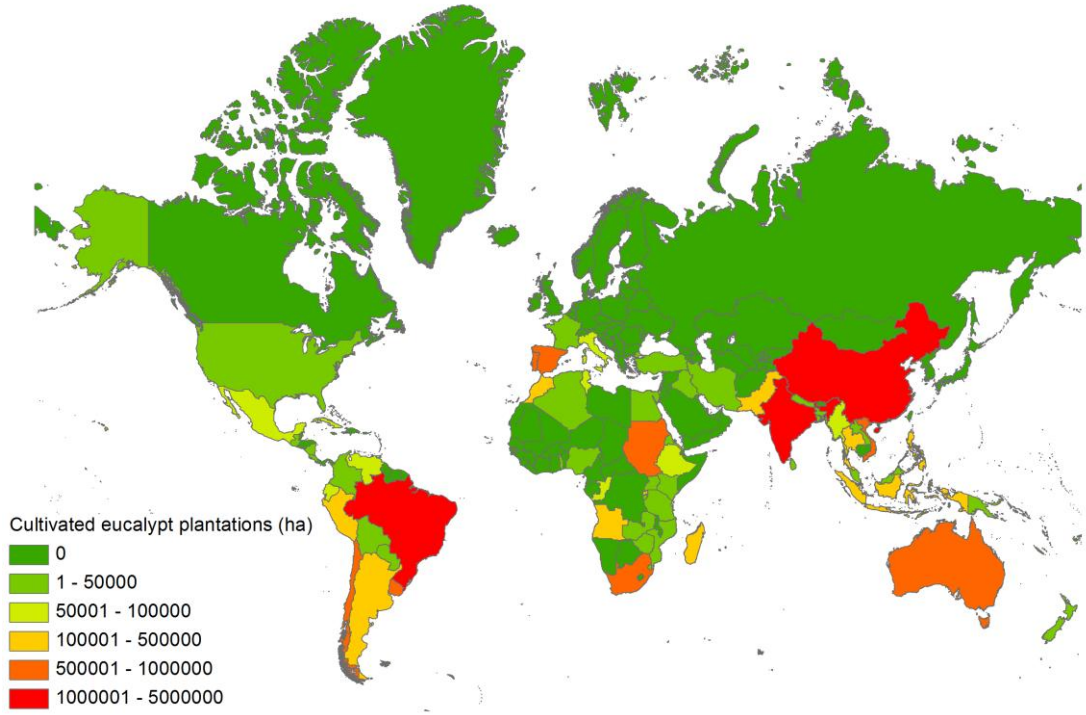

Fig. 1. Distribution of the cultivated eucalypt plantations worldwide adapted from Iglesias Trabado and Wilstermann (2008)

The impact of forest plantations depends on the tree species, intensity of management, the region, climate conditions and type and extent of other management practices in the surrounding landscapes (Martín-Queller et al., 2013). This comprises so many variables, that the research results cannot be extrapolated from the tropical regions to Europe or even from Northern Europe to the Mediterranean Basin.

1.2. Mediterranean basin

1.2.1 Biodiversity

The Mediterranean region is recognised as a worldwide biodiversity hotspot, with a high number of endemic species and high biodiversity (Médail & Quézel, 1999; Mittermeier et al., 1998; Reid, 1998). The importance of this region, which covers only 1.6% of the world surface, is shown by the number of species it hosts - 10% of the world's vascular plants of which 50% are endemic and almost 1000 land vertebrate species (Blondel et al., 2010). In addition, there are 355 reptile species and 106 amphibians, of which 48% and 64% respectively are endemic (Cox et al., 2006), more than 25% of the mammal species are also endemic (Myers et al., 2000) and over 13% of birds are unique to this basin (Myers et al., 2000).

The drivers of this biodiversity are multiple: biogeography, geological history, landscape ecology, and human history (Blondel et al., 2010). The Mediterranean basin has a very distinctive geographical position: it is at the crossroads of Europe, Asia and Africa, and due to climate changes since the Mesozoic, it has been a fertile place for taxa interaction, hybridisation and for speciation to flourish (Blondel et al., 2010). Geographic isolation promoted by tectonic microplate movements has also led to species differentiation, although the precise period in history is uncertain (Blondel et al., 2010). There is evidence that during the last glaciation, the Mediterranean basin acted as a refugium for several taxa because much of central and northern Europe presented unfavourable conditions for the persistence of fauna and flora. For floristic species, the Mediterranean area became a refuge for relict plants but also favoured the emergence of new taxa, being classified as a phylogeographical hotspot (Médail & Diadema, 2009). Between interglacial periods, some of these taxa would disperse again to the northern regions without leaving the Mediterranean area, like the barbastelle bat (*Barbastella barbastellus*) for instance (Rebelo et al., 2012).

A typical characteristic of the Mediterranean region is its patchy, mosaic landscape, with a larger number of dynamic land uses and land covers that promote recurrent colonisations and extinctions at a landscape scale. Most of this dynamic landscape is orchestrated by man, however, there is no consensus on the influence of man on biodiversity. Two schools of thought prevail: one defends the "Ruined Landscape" or

“Lost Eden ” theory, claiming that humans have destroyed the extensive forests that once covered all of the Mediterranean basin leading to desertification (Blondel, 2006). The other suggests that this region was never covered by dense forests, supporting this with paleoecology studies (De Beaulieu et al., 2005). Nevertheless, both theories support the crucial role of man shaping the Mediterranean landscape and the influence on today’s biodiversity. For almost 10000 years, man has been a constant presence in the region designing and redesigning the landscape repeatedly, so some researchers talk about a “co-evolution” between the Mediterranean ecosystem and land-use practices (Di Castri et al., 1981; Makhzoumi & Pungetti, 2005). The destruction of forest is often associated with periods of expansion of the Egyptian, Persian and Greek civilizations and their subsequent decline promoting the recovery of forested areas (Tomaselli, 1977). The degree of recovery is associated with regional climatic conditions, geological type and ecosystem resilience, so the succession for Mediterranean ecosystems is not linear and follows different trajectories (Blondel et al., 2010). However, two main consequences seem to be generalised across the region with a history of human intervention over at least 10000 years. The first is the replacement of deciduous trees by evergreen sclerophyllous shrubs and trees in a patchy landscape (Blondel et al., 2010). The second consequence is the desertification with the disruption in water balance in many deforested areas, leading to soil erosion (Blondel et al., 2010; Houerou, 1977). The high biodiversity in Mediterranean forest has been linked with an “intermediate level of disturbance”, be it grazing, fire, or water management (Naveh, 1982; Torras & Saura, 2008).

1.2.2 *Montados*

These disturbances along with different land uses developed particular landscape designs, the agrosilvopastoral called the *dehesas* and *montado* systems, which cover over 6 million ha in the Iberian Peninsula, are totally dependent on agricultural management (Bugalho et al., 2011; Halada et al., 2011). Extensive grazing of natural pastures, cereal cropping, and production of non-wood products such as mushrooms, berries and cork are some of the activities developed in these systems (Fig. 2).

This savannah-like habitat consists of cork oak (*Quercus suber*), Holm oak (*Q. ilex*) and sometimes deciduous oaks such as *Q. faginea* or *Q. pyrenaica*, in a very low density of 20 to 40 trees per hectare. Although it is not a highly productive system, it is well adapted to the Mediterranean climate, as it shows higher water storage capacity and total soil porosity associated with higher organic matter, when compared to open areas (Marañón et al., 2009).

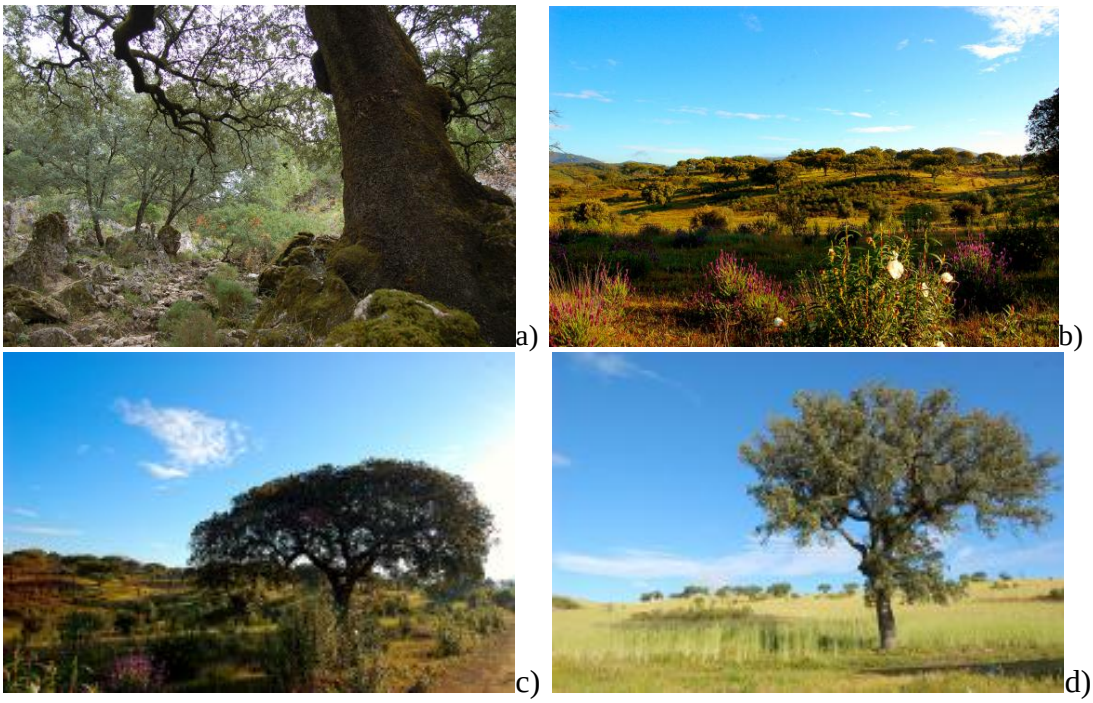

Fig. 2. Examples of *montados* in the study area: a) oak woodland with developed understorey vegetation; *montado* (b and c) with a sparse understorey scrubland, grazed by cattle; d) another example of *montado* with wheat crops as other use

Threats

Nowadays, *montados* and the typical Mediterranean habitats face several threats: land abandonment, intensification of agriculture (Sokos et al., 2013), climate change, invasive species, wildfires (Acácio et al., 2009), afforestation, and replacement of cork stoppers by plastic stoppers (Ahlheim & Frör, 2011), with a consequent reduction in area over past decades (Costa et al., 2011; Debussche et al., 1999). Land abandonment usually leads to the proliferation of woody plants and disappearance of open areas and their characteristic species (Otero et al., 2013). Grazing, prescribed fire or mechanical controls are essential in order to control wildfires. These have

increased in number and intensity over past decades due to fuel accumulation resulting from land abandonment (Moreira & Russo, 2007).

Land abandonment has also been linked with increasing numbers of wild ungulates such as red deer (*Cervus elaphus*) and the decrease of small game species, such as rabbit (*Oryctolagus cuniculus*), Iberian hare (*Lepus granatensis*) and red-legged-partridge (*Alectoris rufa*), due to scrub encroachment of the areas (Vargas et al., 2007) and agriculture intensification with larger fields and destruction of hedgerows (Delibes-Mateos et al., 2009; Sarmento et al., 2012). This is a source of major concern since these species, especially the rabbit - considered a keystone species in southern Europe (Delibes-Mateos et al., 2007) -, are the main prey for threatened species like the Iberian lynx (*Lynx pardinus*), the imperial eagle (*Aquila adalberti*) (Delibes-Mateos et al., 2009) and the wildcat (*Felis silvestris*) (Lozano et al., 2007).

Land abandonment has also led to an increase in afforestation. Open-habitat species are replaced by forest-species and although this might be positive if the former are target conservation species, plantations are preferred by generalist species with a wide distribution and low ecological requirements (Pienkowski et al., 1998). Species across different taxa are negatively affected by land abandonment such as *Podarcis hispanica, Psammodromus hispanicus, Otis tarda, Tetrax tetrax, Alauda arvensis, Lanius collirio* or *Oryctolagus cuniculus* (Russo, 2006).

Habitat alteration also comprises agriculture intensification. The reduction of specialised manual labour, increased mechanisation, strong decrease in crop cultivation, and increased use of fertiliser and agro-chemicals have all been described as important threats (Moreno & Pulido, 2009). This intensification has had an effect on water quality and quantity, on land use, and on soil quality (Stoate et al., 2009). Hedgerows are essential for the supply of food and shelter (Pereira & Rodríguez, 2010), and they maintain stable temperatures, water content and organic carbon (Sánchez et al., 2010). The number of Mediterranean temporary ponds, a priority habitat under the EU Habitat Directive, is decreasing due to agriculture intensification and the species dependent on these ponds are threatened (Gallego-Fernández et al., 1999). Subsidies under the Common Agricultural Policy have also led to the substitution of extensive grazing for a semi-intensive management regime

and replacement of sheep with cattle, with stocking rates similar to the more productive Northern European systems, leading to overgrazing and increase of livestock numbers with adverse consequences for biodiversity (Moreno & Pulido, 2009).

The Mediterranean basin is considered the European region most likely to suffer from the impact of future climate change, with a projected reduction in precipitation and increase in temperature (Schröter et al., 2005) leading to the greatest biodiversity loss worldwide (Sala et al., 2000). Several predicted climate change scenarios for some animal groups show that their area of distribution will contract (amphibians: D'Amen et al. (2011); plants: Klausmeyer and Shaw (2009); Malcolm et al. (2006)). Climate change may also have additional impacts including wildfire intensity and frequency (Pawson et al., 2013). The consequences of this increasing wildfire frequency is an expansion in scrubland of pyrophites species, like *Cistus* sp., which have an allelopathic effect, inhibiting seedling survival and germination (Acácio et al., 2009).

1.2.3 Eucalypt plantations in the Mediterranean region

In the Mediterranean basin, around 32% of forest areas are planted forest, 34% of which are introduced species (FAO, 2010a). These numbers may have a major impact on the economies of these countries; for instance, forest products (mainly paper and cork) represent 10% of Portuguese exports (AEP, 2008). More than one-third of mainland Portugal is covered by forest (35%); eucalypt is the dominant tree (26%) (Fig. 3), and both Maritime pine (*Pinus pinaster*) and native cork oak occupy 23% each (ICNF, 2013). Most of the popular media and general population relate eucalypt plantations to biological deserts and blame those for the expansion and intensity of mega-fires over the past ten years, leading to passionate debates between those holding opposing views (Paiva, 2013; Pereira dos Santos, 2013). Only a few papers have been published in peer-reviewed journals concerning eucalypt plantations and the impact on biodiversity in Mediterranean countries (Proença et al., 2010; Vences, 1993; Zahn et al., 2009). Research papers dating back to the late 1970s state the need to limit the eucalypt expansion to areas with low biological value around the Mediterranean region due to the degradation and destruction of

typical Mediterranean scrubland (Tomaselli, 1977). There is a lack of data regarding the impact of eucalypt plantations on biodiversity, which species are most affected and which management guidelines should be adopted to improve species richness.

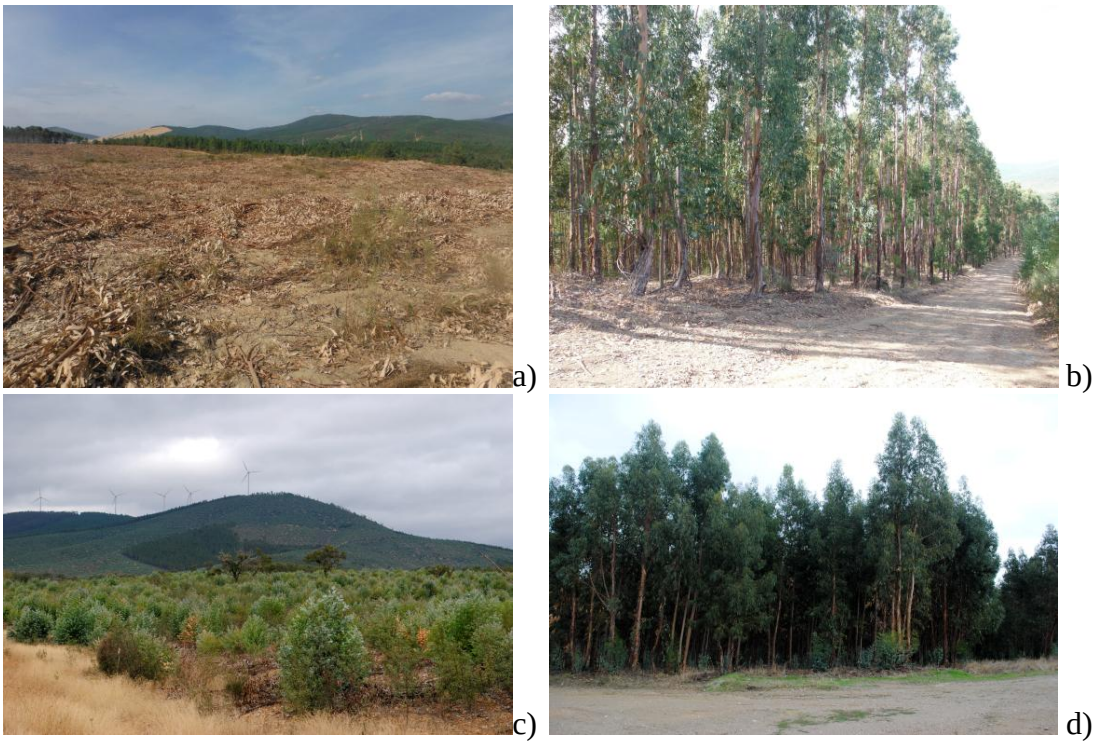

Fig. 3. Eucalypt plantations in the study area: a) view of a clear-cut area; b) a 10-12 year old plantation; c) a one-year old plantation; d) a six-year old plantation

1.3. Focal species

Lambeck (1997) identified "focal species" as a "suite of species, each of which is used to define different spatial and compositional attributes that must be present in a landscape and their appropriate management regimes". The use of focal species is common in research as these species can be treated as surrogate species which cover the needs of threatened species present in the landscape. Three focal faunal groups have been considered here – amphibians, bats and carnivores – with the aim of evaluating the impact of planted forests due to their ecological requirements.

The choice of amphibians as a focal group to evaluate the impact of eucalypt plantations and pond characteristics was based on their particular ecological requirements described in the next section, the susceptibility to both local and landscape variables due to their dual life stages (aquatic and terrestrial), the already

known influence of plantations on amphibian species richness and abundance as well as the lack of research relating eucalypt plantations and amphibian occurrence in the Mediterranean region (Vences, 1993).

Bats were chosen as a focal group due to their importance in the control of insects in agriculture and forestry, their biological traits, described in detail in the next sections, and because little is known about the impact of exotic eucalypt plantations on bat species richness and activity and in which way the different age stands, influence this group in the Mediterranean region.

Finally, carnivores were chosen because of their role as flagship species, the importance on the food web as top predators and also for the lack of knowledge of how land use change may affect the relationship amongst species.

Below, I summarise each group and describe how non-native eucalypt stands and forest practices may impact on the occurrence and species richness of the three groups. I also highlight the lack of knowledge on the influence of eucalypt plantations by these focal groups in the Mediterranean region and the need to assess this in order to mitigate habitat alteration as one of the major threats in the region.

1.3.1 Amphibians

There are more than 6400 amphibian species worldwide, representing nearly 0.5% of all animal species of which one third are globally threatened or extinct (IUCN, 2013). The Mediterranean region has a high diverse amphibian fauna, and the largest proportion of endemism worldwide (69% of urodeles and 56% of anurans) (Wells, 2007). In Europe, nearly a quarter of amphibians are considered Threatened, all of which are endemic species, and a further 17% of amphibians are considered Near Threatened (Temple & Cox, 2009). The major threats identified are habitat modification and destruction (Adams, 1999; Rowley et al., 2009), commercial over-exploitation, introduced species (Adams, 1999; Knapp, 2005; Maret et al., 2006), environmental contaminants, global climate change (D'Amen & Bombi, 2009), and emerging infectious diseases, especially the chytrid fungus *Batrachochytrium dendrobatidis* (Murray et al., 2009).

Aquatic-breeding amphibians are of special research interest due to their singular morphological and physiological traits and ecological role (Semlitsch et al., 2009). Firstly, amphibians are the smallest of terrestrial vertebrates, which when coupled with their permeable skin, can make this one of the most vulnerable groups to changes in water quality and droughts. One of the advantages of being small is the ability of some species to persist in very small areas, like wheel tracks. Species like the natterjack toad (*Epidalea calamita*) can even reproduce and eventually complete an entire metamorphosis in such environments. The small body size of species in this group is also correlated to a limited ability to disperse, making them more vulnerable to landscape fragmentation. The fact that the amphibians have permeable skin can also make them more susceptible to desiccation, although it can also be viewed as a key to their success (Wells, 2007). They can rehydrate quickly when water becomes available and make use of their skin for respiration. They need a relatively cool, moist habitat due to their limited physiological mechanisms to prevent water loss to maintain high moisture levels (Owens et al., 2008). Secondly, many species make use of different habitats, according to different stages of their life cycle. Most commonly, they have an aquatic larval stage and a terrestrial adult stage, but they can use different habitats for reproduction, feeding and hibernation, becoming more vulnerable to habitat degradation (Wells, 2007). Finally, due to their role in food webs acting as both predator and prey, they are responsible for an important fraction of animal biomass available to other trophic levels (Dodd, 2010).

Forestry practices have been related to low diversity and abundance of amphibians mainly affecting forest specialist species, due to land cover disturbance, alteration of microclimates, and exposure during their terrestrial phase (Adum et al., 2012; Freidenfelds et al., 2011; Karraker & Welsh Jr, 2006; Popescu & Hunter, 2011; Popescu et al., 2012). Practices such as clear-cutting may lead to higher surface temperature and loss of soil-litter moisture (Semlitsch et al., 2009), altering migration behaviour (Todd et al., 2009), decreasing survival and poor body condition (Todd & Rothermel, 2006) and, ultimately, leading to species extirpation in the area (Dupuis et al., 1995; Petranka et al., 1994). Where these management practices are conducted within a non-native forest environment, such as one dominated by eucalypt, the consequences may be exacerbated (Russell & Downs, 2012). Eucalypt has been associated with altered soil conditions, leading to both lower pH in soil

(Jobbágy & Jackson, 2003) and water, disturbing the viability of the aquatic macroinvertebrate community – amphibians' main prey (Canhoto & Laranjeira, 2007) - and water depletion (Mendham et al., 2011). Changes in soil and land characteristics may have a negative impact during aestivating and overwinter periods, especially on fossorial species.

Amphibian adult migration and juvenile dispersion are influenced by structural connectivity, i.e. the physical characteristics of the landscape structure, as well as by functional connectivity, i.e. the species' response to the physical characteristics varying between species in the same landscape and within species in different landscapes (Tischendorf & Fahrig, 2000). Adult migration is defined as "movements, primarily by resident adults, toward and away from aquatic breeding sites", while juvenile dispersal is "unidirectional movements from natal sites to breeding sites that are not the pond of birth and not part of the local population" (Semlitsch, 2008), and therefore usually greater than migration distances. However, both are species-specific and individual-specific and influenced by an ability to overcome predation, challenging microclimatic conditions and movements of the substrates (Fahrig, 2001; Janin et al., 2012; Mazerolle & Desrochers, 2005). Nevertheless, not only landscape processes affect amphibians' population dynamics. At the local scale, pond characteristics also restrict the occupation by certain species. Presence of aquatic vegetation promoting microhabitat heterogeneity and the absence of exotic predator fish may favour a diverse amphibian community.

1.3.2 Bats

For the Mediterranean region, it has been described 55 bat species, of which 7 are endemic and the same number are threatened (Temple & Cuttelod, 2009). In the region, the major known threats for this faunal group are habitat destruction and modification (loss of forests, intensive agriculture and pesticide use, pollution), roost site disturbance (loss of trees, of buildings, of underground habitats), persecution and lack of information (Hutson et al., 2001; Temple & Cuttelod, 2009). The control of insects in agriculture and forestry is one of the most important ecosystem services played by this group. Boyles et al. (2011) estimated that the value of bats to the agricultural industry in the United States for 2007 was around 22.9 billion dollars,

just for the reduced costs of pesticide applications and not its resulting impact on the ecosystem. The biological traits of bats, such as high dispersal ability, late sexual maturity, slow population growth and also frequent dependence on specific habitats for foraging or roosting and their role in the food web, mostly as insect predators, make them a group of special research interest concerning habitat loss and alteration, such as eucalypt plantations.

Forest composition and structure have a major influence on bat habitat quality because influence the availability and accessibility of roosts and prey (Hayes & Loeb, 2007), predator avoidance (Baxter et al., 2006) and animal movement (Jung et al., 2012). The importance of wing morphology and body mass on flight speed and manoeuvrability, which influences the availability of foraging habitat has often been described (e.g. Aldridge & Rautenbach, 1987; Armitage & Ober, 2012; Norberg & Rayner, 1987). Small bats, with low wing loading and aspect ratio, are characterised by slow flight and high manoeuvrability, adapted to flying among vegetation (Aldridge & Rautenbach, 1987). Physical clutter is likely to affect the ability of bats to move freely through a habitat and may also increase background echoes and make it more difficult to accurately detect and capture prey (Brigham et al., 1997). Some authors suggest that stand clutter is more important than prey availability in determining habitat use by fast-flying bats (Armitage & Ober, 2012; Grindal, 1996). Very dense clutter, even with greater insect abundance, has been shown to affect both capture success and capture time, making these areas also unsuitable for gleaning and hawking species (Adams et al., 2009; Rainho et al., 2010; Smith & Gehrt, 2010; Titchenell et al., 2011; Webala et al., 2011). The impact of eucalypt plantations and use of different age stands by bats have been studied in Australia (e.g. Hobbs et al., 2003; Law et al., 2011), however, despite its widespread use as a plantation tree, little equivalent research has been done outside the native range of eucalypts, even in biodiversity hotspot areas such as the Mediterranean basin (Goiti et al., 2008).

1.3.3 Carnivores

Carnivores are one of the most charismatic groups, comprising over 285 species, with one third of species Threatened or Near Threatened (IUCN, 2013). In the

Mediterranean region, there are 36 species, two are endemic and 14 are threatened (Temple & Cuttelod, 2009). Habitat loss and fragmentation, poaching, inbreeding depression, hybridisation, disease and prey scarcity are some of the known threats.

Carnivores have long been used as flagship species, like the tiger (*Panthera tigris*) or the giant panda (*Ailuropoda melanoleuca*) (Caro, 2010). As predators they interact with other species and their decline or loss can have a significant impact on structure and functionality of the ecosystem (Duffy, 2003). The presence of a biodiverse carnivore community is often regarded as a sign of a healthy ecosystem (Miller et al., 2001). In the Mediterranean region, carnivores are most threatened by prey scarcity, especially wild rabbit, a keystone species in this region, and habitat destruction and alteration by replacing extensive use of the land with intensive agriculture and afforestations with exotic species like eucalypt. These threats can lead to modifications in the way in which carnivores interact with each other. The intraguild predation theory predicts that top predators distribute themselves according to food availability and subordinate predators according to food availability and safety from predation (Holt & Polis, 1997). Niche partitioning among carnivores is essential for coexistence (Schoener, 1974). This differentiation can take several dimensions: differential use of food resources (Foster et al., 2013), prey size, diel patterns (Schuette et al., 2013), space and habitat use (Sarmento et al., 2011).

In Mediterranean ecosystems, relationships among sympatric carnivores have been studied extensively; however, the impact of major land use change, such as plantation forestry, on niche partitioning and intraguild predation is less well understood. Eucalypt plantations represent open habitats, with low understorey complexity (Ramírez & Simonetti, 2011) that offer inadequate shelter from extreme weather conditions and other predators (such as dogs or man) (Mangas et al., 2008) and where food availability is low (fruits, insects and small mammals) (Pereira et al., 2012; Rosalino et al., 2005). Resource availability controls predator interactions: it is expected that as resources decline there will be an increase in interference interaction – direct killing – due to hungry predators moving more in search of prey, increasing the rate of encounters with subordinate carnivores (Polis et al., 1989).

1.4. The thesis

In this thesis I investigate the impact of eucalypt plantations on biodiversity, using amphibians, bats and carnivores as focal groups.

1.4.1 Study aims

Despite the high rate of dispersion worldwide of the eucalypt as the main tree for short-rotations plantations, little is known about the impact of this tree on biodiversity in the Mediterranean region. One of the probable reasons is its localised geographical distribution in the region, mainly in Portugal and Northern Spain. Nevertheless, the Iberian Peninsula hosts 30% of endemic European plant and terrestrial vertebrate species (López-López et al., 2011), and there is an urgent need to assess the level of impact of eucalypt plantations on biodiversity.

The main objective of this thesis is to investigate the impact of eucalypt plantations on species richness and species-specific occurrence of amphibians, bats and carnivores. Specifically, I aim to understand if amphibian species occurrence is influenced by local characteristics (micro-scale), land-use cover (migration and dispersion-scale) or a mix of both and whether the effects differ if the main cover is eucalypt plantations or *montado*. I also aim to understand if bat activity and species richness are influenced by plantation age stands, due to their particular structure, and if the response variables behave similar in mature stands and native *montados*. Finally, I aim to understand if the carnivore community occupancy and detection and species interaction are affected by eucalypt plantations. Based on my findings, I recommend some management actions that can be adopted to enhance biodiversity in intensive-managed eucalypt plantations in the Mediterranean region.

1.4.2 Thesis structure

In this chapter, I introduced the concept of forest plantation and its expansion worldwide, the impact of plantations and common silvicultural practices on biodiversity as well as the eucalypt as the tree of choice. I also described the Mediterranean basin as a biodiversity hotspot, the native agrosilvopastoral *montado* and the local threats. Finally, I provided some justification for the choice of the three focal groups used in the study – amphibians, bats and carnivores.

In Chapter 2, I assess the influence of the landscape and local variables on the presence of amphibians in ponds distributed in *montados* and eucalypt plantations, considering three scales – local (pond), intermediate (400 metres buffer), and broad (1 km buffer) scales, individually and in combination.

In Chapter 3, I compare the overall bat activity, species richness and Kuhl's bat (*Pipistrellus kuhli*) (the most abundant bat species in the area) activity between eucalypt plantations (age stands: clear-cut, plantations with 3-6 years and mature plantations, with 12-16 years) and native *montado*, and examine the influence of stand, landscape and survey variables within plantations on the response variables.

In Chapter 4, I test the impact of eucalypt plantations on niche partitioning in a carnivore community consisting of red fox (*Vulpes vulpes*), badger (*Meles meles*) and stone marten (*Martes foina*). Based on data from camera trapping, I evaluate the influence of eucalypt plantations on species occupancy and detection in single-species and co-occurrence models and on temporal activity.

In Chapter 5, I summarise the results and discuss their implications for plantation management and biodiversity, as well as considering future avenues for research.

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CHAPTER 2

Exotic fish in exotic plantations: a multi-scale approach to understand amphibian occurrence in the Mediterranean region

Preface

Silvicultural practices have been related to low diversity and abundance of amphibians mainly affecting forest specialist species, due to disturbance, alteration of microclimates, and exposure during their terrestrial phase (Adum et al., 2012; Freidenfelds et al., 2011; Karraker & Welsh Jr, 2006; Popescu & Hunter, 2011; Popescu et al., 2012). Eucalypt plantations, in particular, have been associated with lowering soil pH (Jobbágy & Jackson, 2003) and water depletion (Mendham et al., 2011) which may affect negatively amphibians, when they migrate or disperse, during their terrestrial stage. Nevertheless, not only landscape processes affect amphibians' population dynamics. At the local scale, pond characteristics, such as aquatic vegetation and presence of predatory fish, also restrict the occupation by certain species.

In this Chapter, I aim to determine the environmental factors that influence the species occurrence and species richness, in 88 ponds, in a landscape dominated by eucalypt plantations and by traditional use (agricultural, *montado* and native forest). I considered variables at three different scales (local, 400 m radius buffer and 1000 m radius buffer) and took into account pond characteristics, land cover and connectivity measurements. I used a generalised linear mixed model (GLMM), with a binomial error distribution (to model species occurrence) and a Poisson error distribution (to model species richness).

This Chapter is written in the style of and will be submitted to the journal "PLOS ONE".

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Exotic fish in exotic plantations: a multi-scale approach to understand amphibian occurrence in the Mediterranean region

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Abstract

Globally, amphibian populations are threatened by a diverse range of threats including habitat destruction and alteration. Forestry practices have been linked with low diversity and abundance of amphibians, due to land cover disturbance, alteration of microclimates, and exposure during their terrestrial phase, and these impacts are exacerbated where exotic species are used in forestry. The effect of exotic *Eucalyptus* spp. plantations on amphibian communities has been studied in a number of biodiversity hotspots, but little is known of its impact in the Mediterranean region. Here, we identify the environmental factors influencing the presence of six species of amphibians and species richness occupying 88 ponds in a landscape dominated by eucalypt plantations alternated with traditional use (agricultural, *montado* and native forest) at three different scales: local (pond), intermediate (400 metres radius buffer) and broad (1000 metres radius buffer). We used an information-theoretic approach to select the best model for the six species occurrence and species richness at the three spatial scales and a combination of covariates from the three scales. Thirteen species were detected during the survey, the most common being *Pelophylax perezi*, *Hyla arborea/meridionalis*, *Lissotriton boscai*, *Pleurodeles waltl* and *Triturus marmoratus*, all of which were present in more than half of the ponds. Models with a combination of covariates at the different spatial scales had a stronger support than

those taken individually. The presence of exotic fish in a pond was the most important variable for most of the species occurrence models, having a negative impact on presence, with the exception of *Pelobates cultripes* and *Hyla arborea/meridionalis*. Permanent ponds were preferred by amphibians over temporary ponds. The density of waterlines and/or waterpoints did not increase species occurrence, but the proximity of ponds occupied by their conspecifics did. Eucalypt plantations had a negative effect on the occurrence of the newt *Lissotriton boscai*, and had a positive effect on the presence of *Salamandra salamandra.* Eucalypt plantations had no effect on any of the other species. In conclusion, eucalypts had limited effects the amphibian community at the intermediate and broad scales, but fish introductions had a major impact at all scales. The over-riding importance of fish as a negative impact suggest that forest managers should prevent new fish introductions and eradicate fish from already-occupied ponds whenever possible.

Introduction

Amphibians are one of the most threatened vertebrate groups, with nearly one third of the total number of species now at risk of extinction [1]. Declines in amphibian populations have been attributed to a combination of threats [e.g. 2], including ultraviolet radiation, predation, pollution, invasive species, diseases, habitat alteration and global climate change. In the Mediterranean region, one of the global biodiversity hotspots [3], 29% of amphibian species are threatened with extinction, with habitat alteration and fragmentation cited as the primary reasons for past and future extinctions [1,4].

Although well documented, the amphibian response to land use change is not consistent among species. Some studies have reported lower species richness [5] and reduced abundance [6] in altered landscapes. For example, in Australia, the conversion of eucalypt (*Eucalyptus* spp.) forest to pine (*Pinus radiata*) plantations reduced the number of species detected from eight to two [7], and in the United States, amphibians with high capacity to disperse were more susceptible to fragmentation and local extinction [8]. In contrast, other studies have reported the colonisation of newly altered landscapes by amphibians capable of exploiting

disturbed landscapes. For instance, in Malaysia, oil palm plantations harboured an equal number of species when compared with secondary forest, but a totally different community, with oil palm plantations comprising many more species of least conservation concern [9].

Forest plantations are an example of land use change, expanding 5 million ha per year, between 2000 and 2010 [10]. Forestry practices have been related with low diversity and abundance of amphibians, due to land cover disturbance, alteration of microclimates, and exposure during terrestrial phase, mainly affecting forest specialist species [11-15]. Practices such as clear-cutting may lead to higher surface temperature and loss of soil-litter moisture [16], altering migration behaviour [17], decreasing survival and causing poor body condition [18] and, ultimately, leading to species extirpation in the intervened area [19,20]. A preference for the use of exotic trees in forestry is common worldwide [21]. Eucalypt is one of the most commonly-planted trees in the world [10], and the negative impacts of forestry can expect to be exacerbated in exotic plantations [22]. Eucalypt has been associated with altered soil conditions, leading to both lower pH in soil [23] and water, disturbing the aquatic macroinvertebrate community viability – amphibians' main prey [24] - and water depletion [25]. Changes in the soil and land characteristics may have a negative impact during aestivating and overwinter periods, especially on fossorial species.

The effects of eucalypt plantations on amphibian community have been documented in some biodiversity hotspots outside the eucalypt native range, like Madagascar [26], Brazil [27] and South Africa [22], where species richness is lower when compared to native forests; Costa Rica, where eucalypt plantations were a suitable habitat for the *Eleutherodactylus coqui* [28]; and USA, where the species richness was similar to native forests although differed in composition [29]. However, little equivalent research has been carried out in the Mediterranean basin [30], despite the widespread of eucalypt plantations in the region.

For amphibians, habitat connectivity, defined as "the degree to which the landscape facilitates or impedes movement among resource patches" [31], may be negatively influenced by forest plantations and silviculture practices. Connectivity is crucial for amphibians due to: (1) their distinct habitat requirements for feeding, breeding and

overwintering; (2) an obligatory aquatic reproductive phase; (3) seasonal terrestrial adult migrations which make them susceptible to changes in landscape structure; (4) juvenile dispersal; and (5) their low vagilities and high risk of desiccation. Adult migration is defined as "movements, primarily by resident adults, toward and away from aquatic breeding sites", while juvenile dispersal is "unidirectional movements from natal sites to breeding sites that are not the pond of birth and not part of the local population" [32], and therefore usually greater than migration distances. Most estimates of migration and dispersal distance for the Mediterranean species (or related species) do not exceed 400 and 1000 metres, respectively. There are accounts of individuals exceeding this distance, but most move less than the maximum distance described [33-35]. Land cover, network of ponds and waterlines (ephemeral, temporary and permanent), closeness of ponds occupied with their conspecifics are covariates that can influence amphibians connectivity [36,37]. The proximity and high density of ponds and waterlines may provide a route for migration, facilitating the movements whilst maintaining moist conditions [32]. During migration or dispersal, the preference for occupied ponds by conspecifics is common [36]. However, migration and dispersal are species- and individual-specific and influenced by the ability to overcome predation, challenging microclimatic conditions and the resistance to movements of the substrates [38-40]. Landscape processes are not the only processes to affect amphibians' population dynamics. At the local scale, pond characteristics also restrict occupation by certain species. The absence of exotic fish [41,42], temporary ponds [43] and the presence of aquatic vegetation [44,45] may all favour a diverse amphibian community.

There has been previous research worldwide to investigate local- and landscape-scale variables influencing occurrence patterns in amphibians, [e.g. 46,47], but the results are highly variable [48,49] and region- and context-specific [46,50]. Given the significance of the Mediterranean region for native biodiversity [51], including amphibians, and the predominance of eucalypt forest cover, there is an urgent need to evaluate the impact of these plantations on the amphibian community and assess local and landscape-scale covariates of species occurrence.

Here, we evaluate the impacts of different landscape and environmental factors on amphibian pond occupancy at three different scales, appropriate to the scale of

individual ponds (local), migration distances (intermediate; 400 m) and dispersal distances (broad; 1000 m). Using different scales is useful as different variables may only become significant at a specific scale, improving the quality of the models [46,50,52,53].

At each scale, we tested the hypothesis that all amphibian species would select ponds without fish, with a temporary hydroperiod and with high percentages of aquatic vegetation. At the intermediate and broad scales, we hypothesised that amphibian species occurrence and species richness in a pond would increase with the density of waterlines and ponds, and decline with increasing eucalypt cover and distance to waterlines. Finally, we hypothesised that amphibian species occurrence and richness would be explained better by a combination of covariates across each scale than by covariates at any one scale.

Materials and Methods

Study Area

More than one-third of mainland Portugal is covered by forest (35%). Within this forested area, eucalypt (*Eucalyptus* spp.) is the dominant tree (26%), and both Maritime pine (*Pinus pinaster*) and native cork oak (*Quercus suber*) occupy 23% each [54]. We carried out the study in central-east Portugal, Castelo Branco district (39º40' – 40º10'N, 7º0' – 7º35'W). The area has a Mediterranean climate, with a mean temperature of 16.7ºC (mean minimum: 11.0 ºC; mean maximum: 22.4ºC) and an average precipitation of 758 mm [55].

In the study area, the forest land cover is dominated by eucalypt (*Eucalyptus globulus*) plantations (36%), with different age stands, natural forest of cork oak and Holm oak (*Quercus ilex*), Maritime pine plantations, scrubland areas dominated by *Cytisus* spp., *Cistus* spp. and *Erica* spp. (all comprising 23%), and *montados* (oak savannah-like woodland) (16%). In addition to forestry, the landscape is used patchily for livestock grazing, olive (*Olea europaea*) groves, wheat (*Triticum* spp.) production, and small-scale subsistence agriculture (24%) (Fig. 1). Most of the eucalypt stands are on their third rotation, planted for the first time in the mid-1970s. Each rotation lasts between 12 to 16 years depending on site productivity and

plantations are managed by coppicing. The *montados* in the study area are actively exploited, with cattle grazing and cork extraction.

Field sampling

We collected the data monthly from February to June 2011. We studied 88 ponds, distributed in three major areas (sites A, B and C; Fig. 1).

We sampled the ponds using a combination of three methods: dipnetting, visual surveys, and acoustic night surveys. During each visit, surveys were conducted by two independent observers. Each observer began their surveys at opposite sides of the water body and walked around the perimeter of the pond in the opposite direction, separately recording detections of all life stages of encountered amphibian species. Tree frog *Hyla arborea/meridionalis* tadpoles were identified to genus, because they could not be reliably identified in the field [56]. Sampling effort was proportional to the water point size. Dipnetting was complemented with visual surveys in and around each water point to detect eggs, larvae, juveniles and adults. Amphibians were identified to the species level, whenever possible, using identification keys [57,58]

The visual surveys took place during day and nighttime, the later with the aid of torchlight. For the night survey, we had a 1-minute pause after arrival and then conducted a 3-minute survey, in which we identified each species call, before the visual survey started [33].

Of the 13 species potentially occurring in the region, *Discoglossus galganoi* is the only amphibian species classified by the Portuguese Red Data Book as "Nearly threatened" [59]. All the others are classified as "Least Concern" [59], whilst globally *Pleurodeles waltl*, *Pelobates cultripes* and *Alytes cisternasii* are considered "Near Threatened" by the IUCN Red List of Threatened Species [60].

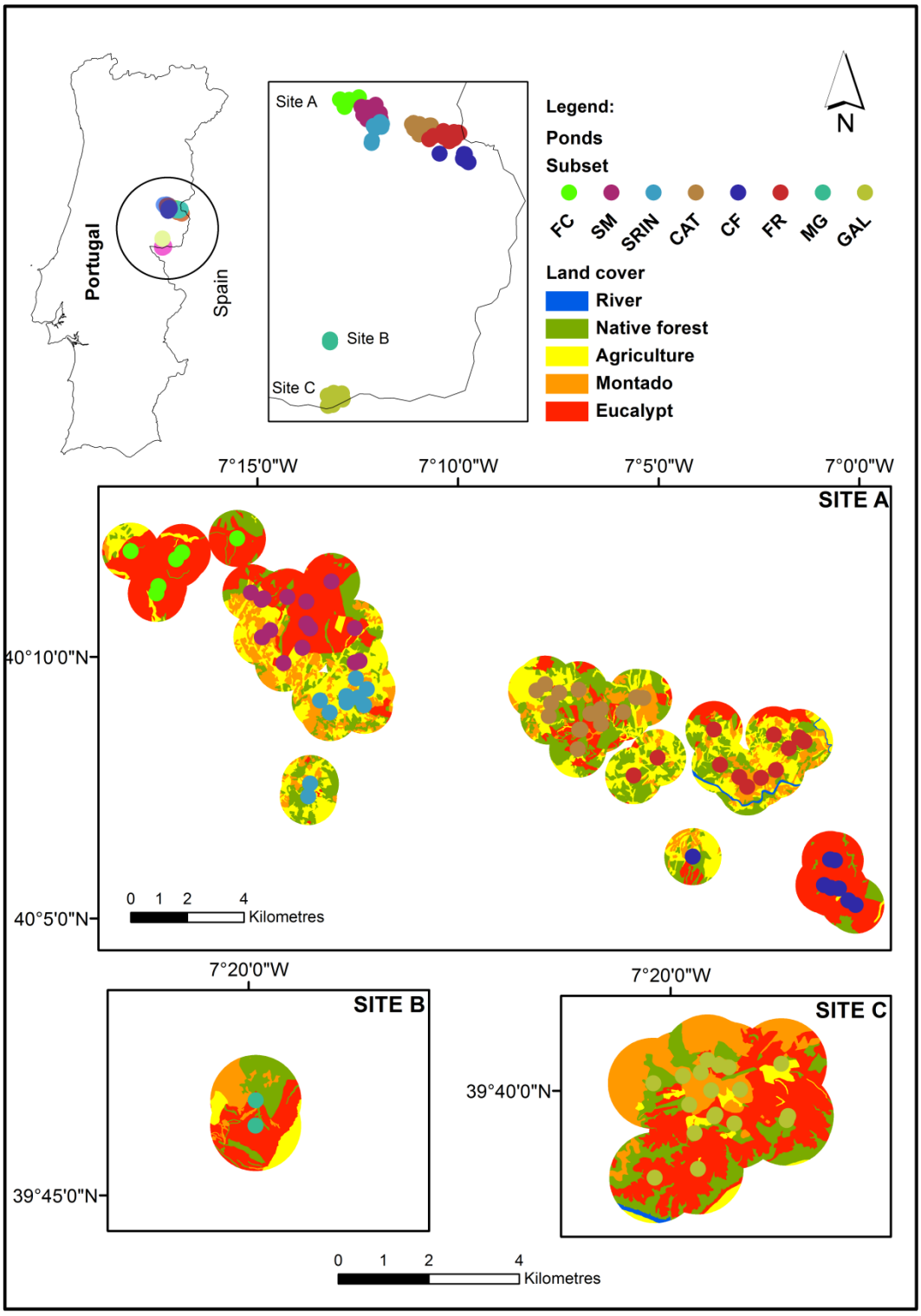

Figure 1. The location of the study area. Distribution of the 88 ponds surveyed monthly between January and June 2011 in central-east Portugal. There were three major study sites distributed in the region: Site A, with 67 ponds; Site B: 2 ponds; Site C: 19 ponds. Each site was divided into subsets (site abbreviations: FC, SM, SRIN, CAT, CF. FR, MG, GAL), according to geographical, topographical or barrier features

Local scale

At each pond, we recorded the presence of predator fish (FISH), the hydroperiod (HYDRO), soil type (muddy or shale) and the percentage of aquatic vegetation [floating (FLOAT), emergent (EMER) and submerged (SUBMER)]. We assessed the presence of predator fish while doing the surveys by visual observation and interviewing the estate managers and recorded the presence of pumpkinseed sunfish (*Lepomis gibbosus*), eastern mosquito fish (*Gambusia holbrooki*) and largemouth bass (*Micropterus salmoides*). These species are non-native to the region and classified as invasive by the national law. We divided the hydroperiod in two levels: temporary (retains water between 3 to 6 months) and permanent (maintains water all year around).

Intermediate scale

Within a 400 m radius buffer of each pond, we measured the proportion of each land cover level [agriculture (AGRIC), eucalypt plantations (EUC), *montados* (MONT) and native forest (NATFOR)], the distance to the nearest waterlines, ephemeral and temporary (NEPH and NTEMP), distance to ponds (NPOND) and density of ephemeral and temporary waterlines (DEPH and DTEMP) and ponds (DPOND). We also measured the distance to the nearest other pond occupied by their conspecifics (NPW, NSS, NLB, NTM, NPC, NHY).

Broad scale

To investigate habitat associations at a broad scale, we assessed the same variables as in the intermediate scale – land cover, the distance to the nearest waterlines, ephemeral and temporary, distance to ponds and density of ephemeral and temporary waterlines and ponds, and the distance to the nearest other pond occupied by their conspecifics - but we applied a 1000 m buffer around each pond.

Model building and model selection

We applied the data exploration techniques described by Zuur et al. [61] to the datasets of species richness and each of the six individual species. We developed models for six out of the thirteen species of amphibians detected: Iberian ribbed newt (*Pleurodeles waltl*) (PW), fire salamander (*Salamandra salamandra*) (SS), Bosca's newt (*Lissotriton boscai*) (LB), marbled newt (*Triturus marmoratus*) (TM), Western

spadefoot (*Pelobates cultripes*) (PC), tree frogs (HY) and species richness. The remaining species were detected only a small number of times, so they were not analysed (Table 1). The same decision was taken for Perez's frog (*Pelophylax perezi*) (PP) but for opposite reasons since it was present in 86 ponds out of 88, then preventing the detection on any environmental trend. To assess collinearity, we used the Spearman rank correlation coefficient |r| because it makes no assumption about linear relationships between two variables [61]; $|r| > \pm 0.6$ was chosen to indicate high collinearity between variables, and where it was found, the variables were not used together in the same model. This value was chosen as a compromise, since the threshold for high collinearity is defined by some authors as $|r| > 0.5$ [61], whereas other authors propose a value of $|r| > 0.7$ [62].

In order to determine whether there was a difference in the studied response variables between eucalypt plantation and other land covers (agriculture, *montados* and native forest), we applied Kruskal-Wallis tests followed by a post-hoc Kruskal-Wallis procedure using the R-package pgirmess [63], based on the algorithm described in [64]. To assess which predictors better explained the behaviour of the response variables, we used a generalised linear mixed model (GLMM), with a binomial error distribution (to model species occurrence) and a Poisson error distribution (to model species richness) with the local subsets as the random variables. The subsets were defined according to geographical, topographical or barrier features (e.g. roads) which created eight local subsets (Fig. 1).

We applied a three-step approach to determine the best top-ranked models (Figure 2). Firstly, we combined all covariates, avoiding multicollinearity, in models (1) at a local scale, (2) at an intermediate scale, (3) at a broad scale, and (4) with combination of the covariates of the different scales in the same models. Secondly, we used data dredge statistics (dredge—MuMIn R package) [65] to run GLMM on those models. Thirdly, we used an information-theoretic approach to select the best model for the six species occurrence and species richness at the three scales and mix-scale [66]. We used the Akaike's information criterion corrected for small sample sizes (AIC_c) in R-package glmmADMB [67] to rank models with $\Delta\ AIC_c$ lower than 2 [66]. If one model attained an Akaike weight of more than 90%, it was considered as the most parsimonious model of all tested models. Otherwise, we calculated

model-averaged estimates and unconditional 95% confidence intervals with multimodel inference [66]. Confidence intervals of the explanatory variables that overlapped zero were considered not statistically significant, so they were not considered for further analyses (i.e. prediction plots or discussion). The relative importance of each variable (rank) was determined by summing the weights for every model where that variable was present [66]. We plotted the variables that were determined to influence the response variables. In order to evaluate the effect size of each predictor variable, we calculated the odds ratio using the multi-average models for each response variable [68].

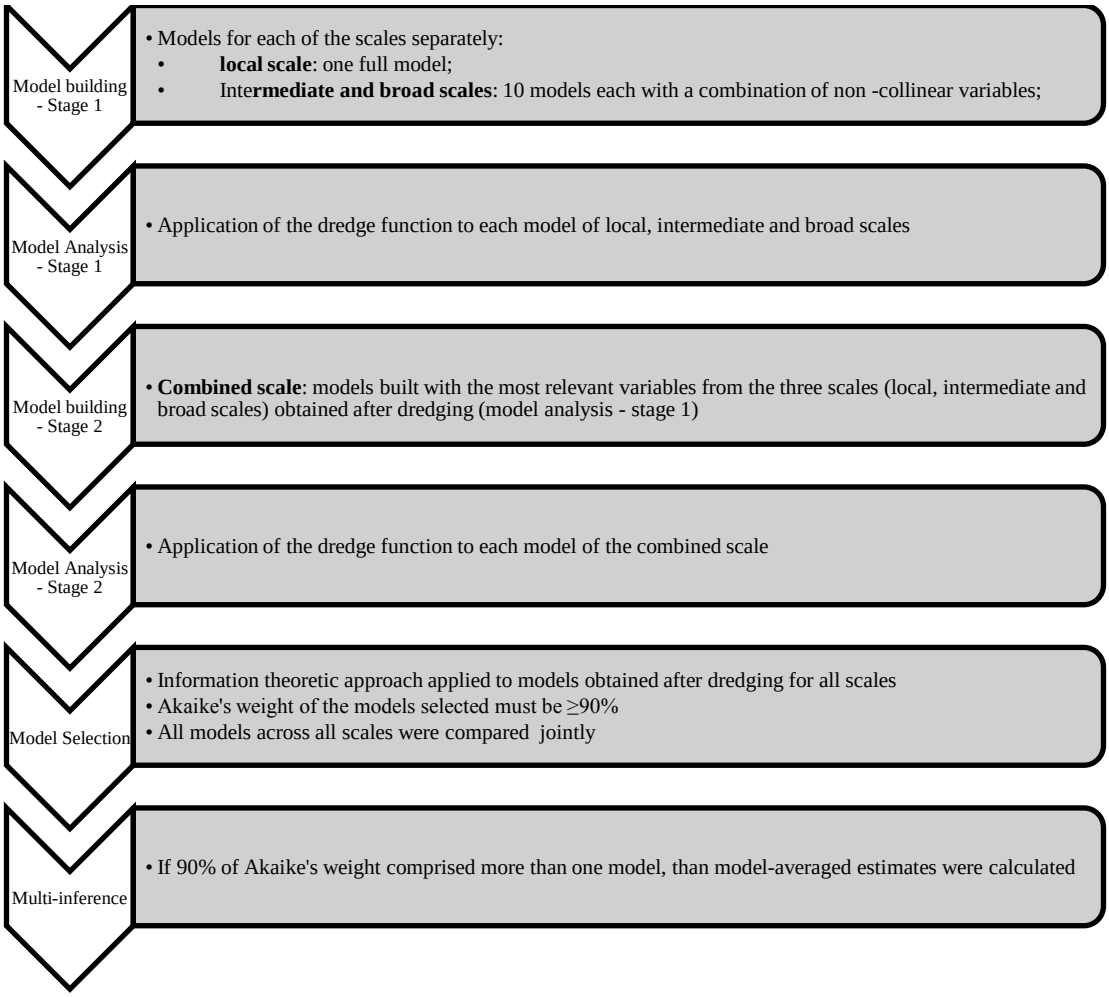

Figure 2. Flowchart describing the statistical analysis applied to the data.

The variance explained (R^2) was calculated as a measure of model fit as described by [69], where marginal R^2 values refer to the variance explained by the fixed factors alone and conditional R^2 is the variance explained by both the fixed and random effects.

Results

Thirteen species were detected during the survey, the most common being *Pelophylax perezi*, *Hyla arborea/meridionalis*, *Lissotriton boscai*, *Pleurodeles waltl* and *Triturus marmoratus*, which were present in more than half of the ponds (Table 1). *Discoglossus galganoi* was only detected once, in a single pond, in the juvenile form.

The highest number of species, eight, was recorded in agricultural and eucalypt stands, at the intermediate and broad scale, respectively (Table 1).

Scale analysis

In this section, we only considered the overall results at each scale, the description of the effects on each species will be done in the next sections. Considering the model-averaged models, at the local scale, presence of exotic fish stood out as the most common covariate, for most of the species, with a negative impact (Table 2 and Table 3, see Table S1 at Supporting Information). The other significant covariates at this scale were temporary ponds (negative), submerged aquatic vegetation with opposite effects on the two species influenced (positive: *L. boscai*; negative: *P. cultripes*) and floating vegetation positively impacting *T. marmoratus*.

At the intermediate scale, of the land cover variables, only eucalypt cover influenced species occurrence, *S. salamandra*, positively (Table 2, Table S1). Density of temporary streams and distance to ephemeral streams were significant with a negative impact on species occurrence (*H. arborea/meridionalis* and *S. salamandra*, respectively) (Table 2 and Table 3, Table S1).

Table 1. Species occurrence and species richness. Presence and percentage (between brackets) of each species and average species richness according to the dominant land cover at each spatial scale (intermediate and broad) of the 88 ponds surveyed and total number of ponds where the species was found.

	AGRIC	EUC	MONT	NATFOR	AGRIC	EUC	MONT	NATFOR	Total
	Intermediate				Broad				
Pleurodeles waltl	21 (81%)	18 (50%)	11 (61%)	7 (88%)	28 (90%)	19 (49%)	7 (64%)	3 (43%)	57 (65%)
Salamandra salamandra	8 (31%)	26 (72%)	2 (11%)	3 (38%)	9 (29%)	27 (69%)	2 (18%)	1 (14%)	39 (44%)
Lissotriton boscai	15 (58%)	28 (78%)	13 (72%)	4 (50%)	18 (58%)	30 77%)	8 (73%)	4 (57%)	60 (68%)
Triturus marmoratus	17 (65%)	22 (61%)	2 (11%)	6 (75%)	23 (74%)	22 (56%)	8 (73%)	4 (57%)	57 (65%)
Discoglossus galganoi	1 (4%)	0 (0%)	0 (0%)	0 (0%)	1 (3%)	0 (0%)	0 (0%)	0 (0%)	1 (1%)
Alytes obstetericans/cisternasii	1(4%)	6 (17%)	3 (17%)	1 (13%)	1 (3%)	6 (15%)	0 (0%)	4 (57%)	11 (12%)
Pelobates cultripes	18 (69%)	9 (25%)	9 (50%)	4 (50%)	23 (74%)	10 (26%)	5 (45%)	2 (29%)	40 (45%)
Epidalea calamita	3 (12%)	6 (17%)	3 (17%)	1 (13%)	4 (13%)	7 (18%)	2 (18%)	0 (0%)	13 (15%)
Bufo bufo	0 (0%)	4 (11%)	2 (11%)	0 (0%)	0 (0%)	4 (10%)	2 (18%)	0 (0%)	6 (7%)
Hyla arborea/meridionalis	25 (96%)	27 (75%)	16 (89%)	6 (75%)	30 (97%)	29 (74%)	10 (91%)	5 (71%)	74 (84%)
Pelophylax perezi	26 (100%)	34 (94%)	18 (100%)	8 (100%)	31 (100%)	37 (95%)	11 (100%)	7 (100%)	86 (98%)
Average species richness average (min-max)	4 (2-8)	6 (2-7)	3 (2-7)	2 (3-7)	6 (3-7)	6 (2-8)	2 (2-7)	2 (2-7)	4 (2-8)
Number of ponds	26	36	18	8	31	39	11	7	88

AGRIC – agricultural; EUC – eucalypt plantations; MONT – *montados*; NATFOR – native forests

At the broad scale, all land covers but *montado* had an effect on species occurrence (Table 2 and Table 3, Table S1). Agriculture with a positive effect on *P. waltl* and *P. cultripes*, eucalypt cover with opposite effects on two species (positive: *S. salamandra*; negative: *L. boscai*) and native forest impacting negatively on *P. cultripes* occurrence. Density of temporary streams and of ponds also had a negative impact on the presence of *L. boscai* at this scale. Distance to the nearest ephemeral stream had a positive effect on *P. waltl* presence and a negative effect on *S. salamandra* occurrence. Distance to the nearest occupied pond by their conspecifics influenced negatively *P. waltl* and *L. boscai* occurrence at both intermediate and broad scales, and *T. marmoratus* exclusively at the broad scale (Table 2 and Table 3, Table S1).

Pleurodeles waltl

P. waltl presence was significantly different between eucalypt stands and agricultural, at the broad scale (Kruskal-Wallis, χ^2 = 14.59, P<0.001). The model selection results provided strong support for a positive relationship between the probability of presence of *P. waltl* and distance to the nearest pond and nearest ephemeral stream, and the proportion of agricultural land at the broad scale. *P. waltl* presence was negatively related to the presence of invasive fish, distance to the nearest other pond occupied by *P. waltl* and the interaction between distance to the nearest ephemeral stream and pond (Table 2 and Fig. 3).

The top ranked two models combined local and broad scale variables and accounted for 95% of the model's Akaike's weight (Table S1). Models at the different scales considered individually had little support (ΔAIC_c>6: ΔAIC_c Broad scale<ΔAIC_c Local scale<<ΔAIC_c Intermediate scale) (Table S1). The intermediate spatial scale models had the weakest support, with the confidence intervals of the covariates density of ephemeral streams, density of temporary streams and proportion of agricultural land all overlapping zero (Table S1). The averaged model and the individual models showed the same results (Table S1 and S2).

Table 2. Coefficient estimates of the model averaged (top-ranked models) for each of the urodels, odds ratio (OR) and respectively confidence interval (CI). Covariate importance between brackets. In bold are the covariates which confidence intervals do not overlap zero. Acronyms are explained in the text.

Covariates	PW				SS				LB				TM			
	β	OR	OR 2.5% CI	OR 97.5% CI	β	OR	OR 2.5% CI	OR 97.5% CI	β	OR	OR 2.5% CI	OR 97.5% CI	β	OR	OR 2.5% CI	OR 97.5% CI
Local (importance)																
FISH	**-2.13 (1)**	0.12	0.03	0.55	**-1.98 (1)**	0.14	0.03	0.68	**-1.71 (1)**	1.81	0.05	0.70	**-1.93 (1)**	0.15	0.05	0.47
EMER													0.92 (0.24)	2.50	0.50	12.81
FLOAT													1.29 (1)	3.63	0.93	14.23
SUBMER									**3.37 (1)**	29.10	3.78	223.90	0.81 (0.19)	2.24	0.37	13.90
Intermediate/broad (importance)																
NPW	**-1.03 (1)**	0.36	0.16	0.82												
NLB									**-0.95 (1)**	0.39	0.17	0.89				

Table 2. Cont.

Covariates	PW				SS				LB				TM			
	β	OR	OR 2.5% CI	OR 97.5% CI	β	OR	OR 2.5% CI	OR 97.5% CI	β	OR	OR 2.5% CI	OR 97.5% CI	β	OR	OR 2.5% CI	OR 97.5% CI
NTM													-0.58 (0.84)	0.56	0.29	1.07
NEPH	**4.39e^{-02} (1)**	1.04	1.00	1.09	**-0.03 (1)**	0.97	0.94	1.00								
NTEMP	-7.98e^{-04} (0.37)	0.99	0.99	1.00												
NPOND	**3.24e^{-03} (1)**	1.00	1.00	1.01												
NEPH:NPOND	**-1.08e^{-04} (1)**	0.99	0.99	0.99												
Intermediate (importance)																
EUC400					**2.94 (0.32)**	18.85	3.39	104.65								
Broad (importance)																
AGRIC1000	**7.24 (1)**	1393.29	16.59	1.17e^{05}												
NATFOR1000					-3.18 (0.29)	0.04	0.0004	4.19								

Table 2. Cont.

Covariates	PW				SS				LB				TM			
	β	OR	OR 2.5% CI	OR 97.5% CI	β	OR	OR 2.5% CI	OR 97.5% CI	β	OR	OR 2.5% CI	OR 97.5% CI	β	OR	OR 2.5% CI	OR 97.5% CI
EUC1000					**3.63 (0.68)**	37.56	4.66	302.76	**-2.76 (1)**	0.06	0.005	0.75				
DTEMP1000									**-0.001 (1)**	0.99	0.99	0.99				
DPOND1000									**-0.27 (1)**	0.76	0.61	0.96				

Table 3. Coefficient estimates (β) of the model averaged (top-ranked models) for each of the anurans and species richness, odds ratio (OR) and respectively confidence interval (CI). Covariate importance between brackets. In bold are the covariates which confidence intervals do not overlap zero. Acronyms are explained in the text.

Covariates	PC				HY				Species richness			
	β	OR	OR 2.5% CI	OR 97.5% CI	β	OR	OR 2.5% CI	OR 97.5% CI	β	OR	OR 2.5% CI	OR 97.5% CI
Local (importance)												
FISH					-1.23 (0.33)	0.29	0.05	1.91	-0.22 (0.89)	0.80	0.64	1.01
FLOAT					1.13 (0.28)	3.11	0.48	2.01	0.13 (0.10)	1.14	0.91	1.44
SUBMER	**-2.78 (1)**	0.06	8.18**e^{-03}**	0.47	2.17 (1)	8.81	0.96	80.88				
HYDRO (temp)	-1.26 (1)	0.28	6.45**e^{-02}**	1.25	**-2.32 (1)**	0.10	0.02	0.53	-0.13 (0.10)	0.88	0.71	1.09
SOIL	-0.47 (1)	0.62	0.13	2.97	0.81 (0.06)	2.25	0.36	14.11				
Intermediate/broad (importance)												
NEPH									-2.4e^{-4} (0.72)	0.99	0.99	1.00
NTEMP	-0.001 (0.41)	0.99	0.99	1.00								
NPOND									-1.5e^{-5} (0.11)	0.99	0.99	1.00
Intermediate (importance)												
AGRIC400									0.25 (0.05)	1.29	0.89	1.85

Table 3. Cont.

Covariates	PC				HY				Species richness			
	β	OR	OR 2.5% CI	OR 97.5% CI	β	OR	OR 2.5% CI	OR 97.5% CI	β	OR	OR 2.5% CI	OR 97.5% CI
MONT400									0.13 (0.02)	1.13	0.76	1.70
NATFOR400									-0.23 (0.05)	0.79	0.45	1.38
EUC400									-0.12 (0.03)	0.89	0.69	1.14
DTEMP400					**-2.2e^{-4} (0.07)**	0.99	0.99	0.99				
Broad (importance)												
AGRIC1000	**5.20 (1)**	182.13	3.25	1.02e^{04}	2.37 (0.37)	10.65	0.002	4.70e^{04}	0.32 (0.22)	1.38	0.90	2.14
MONT1000									0.26 (0.05)	1.30	0.72	2.33
NATFOR1000	**-6.68 (1)**	0.001	3.94**e^{-06}**	0.40					-0.48 (0.05)	0.62	0.26	1.47
EUC1000					-1.75 (0.37)	0.17	0.007	4.36	-0.22 (0.12)	0.80	0.57	1.13
DTEMP1000	3.2e^{-5} (0.21)	1.00	0.99	1.00								

Salamandra salamandra

S. salamandra presence was significantly different between eucalypt stands and agriculture, at the intermediate (Kruskal-Wallis, $\chi^2 = 21.24$, $P<0.001$) and broad scales ($\chi^2 = 18.14$, $P<0.001$); and between eucalypt stands and montado at the intermediate scale ($\chi^2 = 21.24$, $P<0.001$). Models with a combination of covariates from the three different scales provided strong support for a positive influence on *S. salamandra* presence of the proportion of eucalypt (broad and intermediate scale) and a negative influence of fish and distance to ephemeral streams (Table 2 and Fig. 3). The three top-ranked models accounted for 94% of the model's Akaike's weight and considered local, intermediate and broad scale covariates (Table S1). When considered separately, models at each scale had little support, with $\Delta AIC_c>5.5$ (ΔAIC_c Intermediate scale ≈ ΔAIC_c Broad scale << ΔAIC_c Local scale) (Table S1). Some of the covariates measured across the three scales had little support, overlapping zero in their confidence intervals (proportion of native forest at broad scale, distance to pond and to temporary streams, at both temporary and intermediate scale, and hydroperiod and submerged vegetation, at the local scale) (Table S1). The averaged model and the individual models showed the same results (Table S1).

Lissotriton boscai

A single top-ranked model with a combination of covariates from the local and broad scales best explained *L. boscai* presence, accounting for 99% of the model's weight selection (Table S1). The single scale models had a $\Delta AIC_c>10$ (ΔAIC_c Intermediate scale ≈ ΔAIC_c Broad scale << ΔAIC_c Local scale). There was strong evidence of a negative relationship between occurrence of *L. boscai* and the presence of fish, distance to the nearest other pond occupied by their conspecifics, density of ponds and of temporary streams and proportion of eucalypt at the broad scale (Table 2 and Fig. 3).

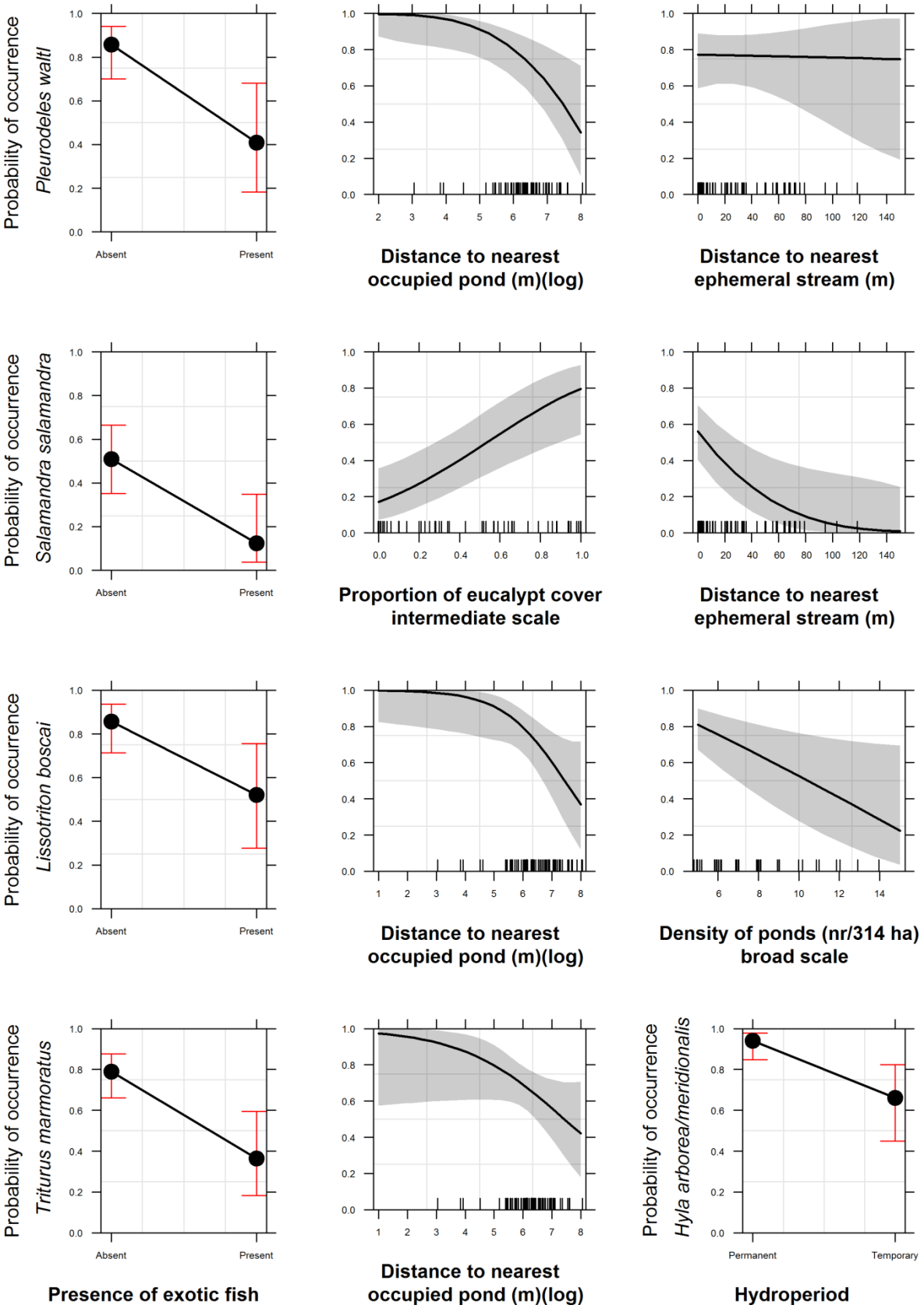

Figure 3. Fitted values predicted by the averaged models for each of the response variables. The dashed line is the confidence interval at 95%.

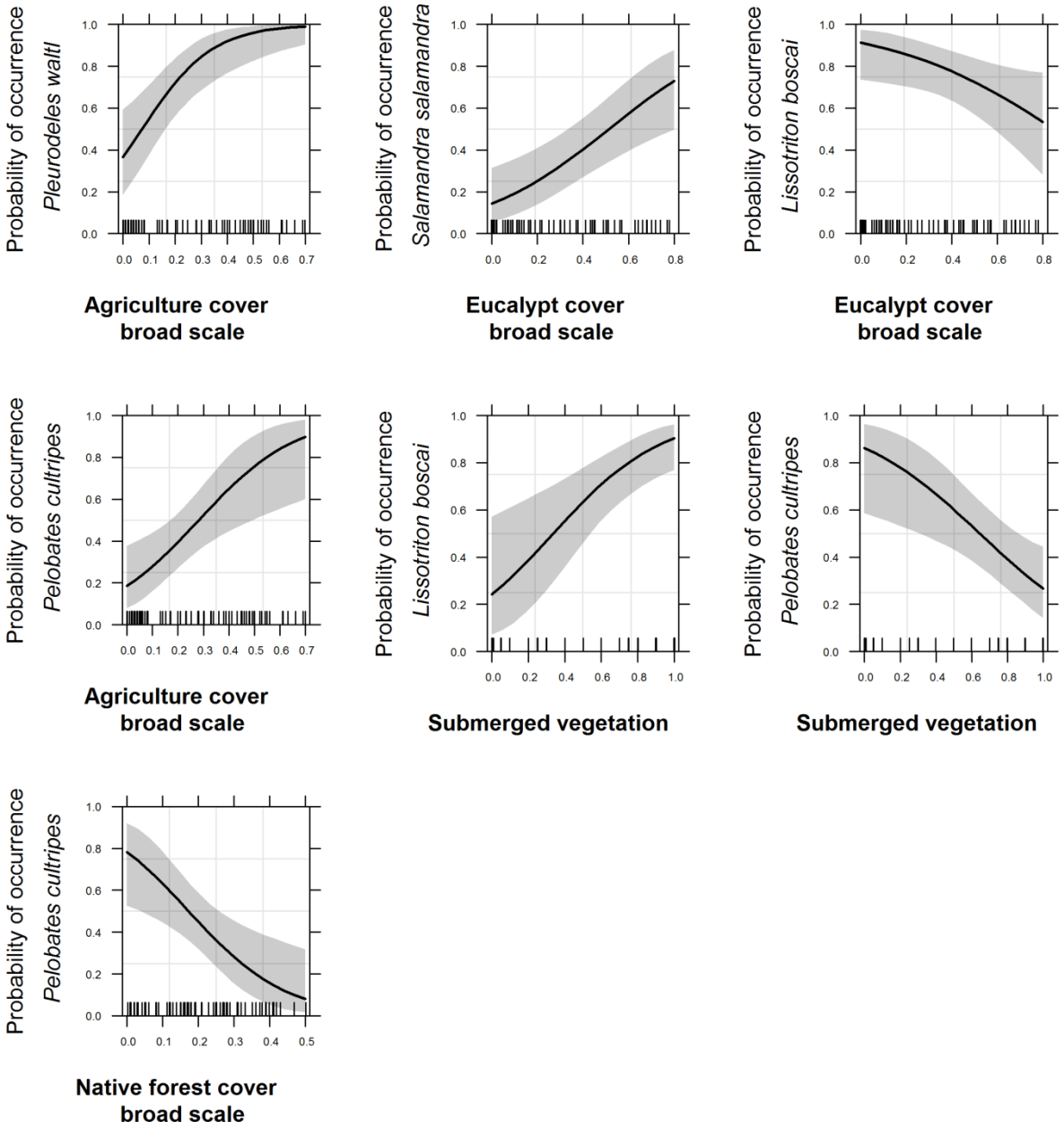

Figure 3. Cont.

The proportion of submerged aquatic vegetation had a positive influence on *L. boscai* presence (Table 2 and Fig. 2). The averaged model and the individual models showed the same results (Table S1).

Triturus marmoratus

Model selection provided high support for a positive relationship of *T. marmoratus* with floating vegetation and a negative relationship with presence of fish and distance to the nearest occupied pond by their conspecifics (Table 2 and Fig. 3). Of the four top ranked

models, three had a combination of covariates at the different scales, and one had covariates exclusively from the local scale, accounting for 92% of the Akaike's weight. There was little support for models at the intermediate and broad scale, with $\Delta AIC_c > 9.9$ (ΔAIC_c Local scale < ΔAIC_c Broad scale ≈ ΔAIC_c Intermediate scale). Fish presence was the only covariate supported on the averaged model, the confidence interval of the others mentioned above overlapped zero (Table S1).

Pelobates cultripes

P. cultripes presence was significantly different between eucalypt stands and agriculture, at both scales (intermediate: $\chi^2 = 12.08$, $P<0.001$; broad: $\chi^2 = 17.11$, $P<0.001$). A combination of local and broad spatial covariates were part of the models that supported *P. cultripes* presence, namely agricultural (positive effect) and native forest cover (negative effect) at broad scale and proportion of submerged aquatic vegetation which reduced this anuran presence (Table 3 and Figure 3). The AIC_c weight of these models, although high (84%), did not reach 90%, which suggests a degree of uncertainty in the models. The remaining scale models had a $\Delta AIC_c > 2$ (ΔAIC_c Local scale ≈ ΔAIC_c Broad scale < ΔAIC_c Intermediate scale). The averaged model and the individual models showed the same results (Table S1).

Hyla arborea/meridionalis

A high number of models – 14 models – with $\Delta AIC_c < 2$ accounted for 89% of Akaike's weight, comprising models of combined scales and models of local covariates (Table S1). There was a positive relationship between *H. arborea/meridionalis* presence and proportion of submerged aquatic vegetation and a negative influence of temporary ponds and density of temporary streams at the intermediate scale (Table 3 and Fig. 3). The intermediate and broad scale models had $\Delta AIC_c > 2$ (ΔAIC_c Local scale < ΔAIC_c Broad scale < ΔAIC_c Intermediate scale). On the averaged model, the confidence interval of the covariate submerged aquatic vegetation overlapped zero, but the density of temporary streams and temporary ponds remained significant (Table 3).

Species richness

Twenty-eight models to explain species richness, from all spatial scales, had a $\Delta AIC < 2$, indicating high uncertainty on model selection, confirmed by the R^2 values (Table S1). Presence of fish was the only covariate that consistently stood out as significantly

important in most of the models (Table S1). Distance to ephemeral streams was significant in a single model, the confidence intervals overlapped zero in the remaining ones (Table S1). Both these covariates had a negative effect on the response variable. All the other covariates had little or no support since their confidence interval overlapped zero. On the averaged model no covariate at any spatial scale had any support (Table 3).

Discussion

Some of our initial hypotheses were supported by our results. At a local scale, exotic fish presence was the most important variable for most of the species occurrence models, with the exception of *P. cultripes* and *H. arborea/meridionalis*, having a negative influence on species occurrence; and models with covariates across the three spatial scales had a stronger support than models taken individually. However, some of our results were contrary to expectations. At the local scale, permanent ponds were preferred over temporary ponds and not all the species were favoured by the increase of aquatic vegetation. At the intermediate and broad scales, density of streams and/or water points did not increase species occurrence and the decrease of distance of the connectivity variables did not show a consistent positive relationship with species occurrence. At the broad scale, eucalypt plantations only affected negatively *L. boscai* occurrence, and had no significant effect on the other species, even favouring the presence of *S. salamandra*.

The negative impact of introduced predatory fish on amphibians has been reported in several studies worldwide [70-75] and in the Mediterranean region [41,42,76,77]. These impacts occur through direct predation, competition or pathogen transfer [77-82]. Certain amphibians may be more susceptible to these threats because they are not usually exposed to predatory fish, either because they are associated with temporary ponds, where fish are absent, and therefore lack appropriate defences [83] or because they do not recognise these fish as threats since they are all non-native species and they had little or no evolutionary history with these predators [82]. Nevertheless, there are amphibians that co-exist with alien fish, and have defence mechanisms either because they may have developed them during the course of evolution and conserve them in the absence of predators or because those mechanisms work against both native and non-native predators [82]. In this situation, tadpoles may show changes in morphological traits (e.g. increased tail area) and in behaviour (lower activity rate, aggregation, higher use of complex aquatic vegetation for

refuge) to adapt to the novel situation besides tadpole unpalatability and/or chemically mediated predator avoidance [84-87]. Presence or absence of fish was irrelevant only for the *H. arborea/meridionalis* and *P. cultripes* occurrence models, although others studies have detected a negative relationship (*P. cultripes*: Beja and Alcazar [56]; *H. arborea*: Bronmark and Edenhamn [74],Hartel et al. [79]). It has been reported in previous studies that these species are more resilient against predator fish due to their morphological traits or morphological plasticity. Specifically, *P. cultripes* larvae attain a large body size (on average around 80 mm, [88]) and *H. arborea* is able to develop deeper tail fins and deeper tail muscles in presence of fish [84]. On the other hand, their swimming behaviour, both nektonic, may increase the chance of being preyed upon by making them more visible to visually oriented fish predators like *L. gibbosus* [79,89-91].

Avoidance of temporary ponds by *H. arborea/meridionalis* has also been reported previously [e.g. 92]. Both species have a long larval stage, on average 3 months [93], and temporary ponds can dry out before metamorphosis is complete [94]. Although temporary ponds cannot support predatory fish, the desiccation risk in the Mediterranean region is high, so the preference for ponds with a long and stable hydroperiod may still improve the recruitment success of these amphibian species [43].

Aquatic vegetation can provide refuge, food [89] and protection against UV-B radiation, which can affect some species during early developmental stages [95]. Four of the studied species occurrences were affected by aquatic vegetation. Newt occurrence in ponds with a high percentage of vegetation (floating vegetation: *T. marmoratus* and submerged vegetation: *L. boscai*) is related to their oviposition habits of wrapping each egg individually in leaves to protect them from UV-B radiation and predators [44]. However, vegetation also provides food and shelter [45], which may explain the preference of *H. arborea/meridionalis* for ponds with a high proportion of submerged vegetation. *P. cultripes* was the only amphibian that avoided ponds with a high percentage of submerged vegetation. This anuran is a good swimmer, and feeds within the water column, and it is possible that too much aquatic vegetation interferes with its foraging.

Connectivity covariates - distance to waterlines or ponds and density of waterlines and ponds - showed different trends amongst the studied species, and only *P. cultripes* and *T. marmoratus* occurrence was not affected by these covariates. The increased probability of

occurrence of a certain species in a pond was often related to a decrease in the distance to the nearest other pond occupied by that same species. Most juveniles urodels do not disperse more than 500 metres from the breeding pond and adults show a high level of site fidelity to the pond they first reproduced in [37]. In fact, juveniles are not well adapted to dispersal. They are smaller, more prone to desiccation and have less locomotor capacity than adults to travel long distances, and they sustain high mortality rates when they leave the pond [32]. Due to all these constraints it is most likely that juvenile urodels disperse to nearby ponds, depending on close "networks" of ponds where the species is already present. Chemical cues, both aquatic and terrestrial, may lead these juveniles to non-natal ponds [36,37]. In a laboratory setting, *L. boscai* preferred water that contained chemical cues of themselves or conspecifics [36]. Heterospecific auditory cues may also attract some species and help with pond orientation. *T. marmoratus* showed positive phonotactic orientation when exposed to *Epidalea calamita* advertisement calls [96], and *Lissotriton helveticus* showed the same behaviour when exposed to *P. perezi* calls [97]. *Triturus alpestris* is capable of long distance homing using only magnetic compass [98]. However, surprisingly, a high density of ponds or of waterlines had a negative impact on *L. boscai* and *H. arborea/ meridionalis* occurrence. Our results are partially coincident with those by Joly et al. [99], with species being more abundant at intermediate pond density.

Both local (aquatic; within-pond) and landscape (terrestrial) features are expected to influence species occurrence. The contribution of each feature may depend on their spatial configuration and quality [100]. Water is a scarce good in Mediterranean regions, so aquatic habitats are expected to act as a constraint to population occurrence and dynamics, with the distribution and characteristics of terrestrial habitats only having a major role when ponds are plentiful [99]. For *L. boscai*, the positive influence of proximity of the nearest occupied ponds by its conspecifics may indicate that this urodel preferentially disperses to ponds where conspecifics are already present.

H. arborea/meridionalis is often associated with ponds with emergent vegetation where they can hide but also display their courtship behaviour, preferring still water to breed [101]. Therefore, a high density of temporary streams, with running water, at the migration scale, may not suit this small size anuran.

S. salamandra is often associated with temporary streams for breeding, avoiding ephemeral streams [102], contrary to our results. This forest species has a long terrestrial phase, using ponds or streams only to deposit their larvae, spending the rest of their time on land. Our results showed also the positive effect of eucalypt plantation at both intermediate and broad scale on the occurrence of this species. Eucalypt plantations place large demands on soil water. In some cases water depletion caused by eucalypts can reach 8 metres depth [25], leading to low levels of moisture at the surface. Eucalypt plantations in the Mediterranean region are also characterised by a lower macro-arthropod abundance when compared to native habitats such as cork oak woodlands, olive groves or riparian vegetation [103]. Despite this, eucalypt plantations apparently favoured *S. salamandra* occurrence, a urodel that has a strong association with high woodland cover [104], and these stands are the only forest-cover type that cover extensive areas in the region. We tentatively interpret this to be a consequence of the proximity of ephemeral streams which may supply sufficient humidity to reduce the risk of desiccation and also serve as a source of prey, especially if the original riparian vegetation is maintained [103], which was verified in most of our study area.

Nevertheless, the conditions that favoured *S. salamandra* had the opposite effect on *L. boscai*. This species, although being one of the most aquatic European newts, makes terrestrial incursions throughout the year and goes into summer dormancy in hot and dry regions [105]. *L. boscai* has a low ecological plasticity [106] and low dispersal ability [44]. Thus, any additional barrier, like chemical fertilisers, soil disturbances and low soil depth can add costs to the distance travelled [39,107]. In addition to the impact of eucalypt plantations in causing soil water depletion, the smaller size of this newt compared with *S. salamandra*, may make it more susceptible to predation and desiccation when crossing extensive areas of exotic stands.

Agricultural land is often associated negatively with amphibian presence due to multiple interventions throughout the year, altering the soil humidity and jeopardizing refuges during aestivation, as well as potentially causing direct mortality due to injuries [108]. The use of fertilisers may also affect the body condition of amphibians and their ability to disperse depending upon concentrations, time of the year and species sensitivity [109,110]. In addition, cattle grazing may have a negative impact on water quality through nitrogenous deposits, increasing eutrophication, degrading water quality but also by

grazing on the shoreline vegetation, that acts as refuge and source of food and oviposition sites [111,112]. However, the agricultural use in the study area is extensive rather than intensive, and comprises olive groves, wheat areas, and small-scale farming for personal use, with low use of fertilisers and grazing at low densities, mainly by cattle. Hence, the practice of small-scale agriculture, which represents an anthropogenic disturbance of only intermediate impact, favoured the occurrence of *P. waltl* and *P. cultripes*, especially at the broad scale. Nonetheless, that was not the case for native forests, which combined pine, oak and mixed forests, and *P. cultripes* avoided these areas. Adult *P. cultripes* need soft soils to dig their burrows and they might have some difficulties digging in forested areas when compared with agricultural land.

Overall, at the local scale, the presence of exotic fish had a strong negative impact on the occurrence of most species. At the intermediate and broad scales, our results suggested that eucalypt did not have a strong effect on species occurrence. The eucalypt stands of the study area were embedded in a traditional agro-forestry matrix, with intermediate disturbance, and a conservative approach must be taken to extrapolate these results to larger extensions of eucalypt plantations surrounded by a degraded matrix, with a high level of disturbance (e.g. intensive agriculture, barriers such as roads). As further research, we suggest the evaluation of functional connectivity. This was not possible in our study because there are only a few studies that relate costs of travelling with habitat structure, and to our knowledge, for some species, there is an absolute lack of information, like for *P. cultripes* or *L. boscai*. The results obtained in this paper can be refined, as future work, by using the information of the different life stages and abundance per effort that were collected during fieldwork. In conclusion, eucalypts had limited effects on the amphibian community at the migration and dispersal scales, but fish presence had a major impact at all scales. Our results highlight the importance of context-dependency in predicting impacts of landscape composition and structure on amphibian populations. However, the over-riding importance of fish as a negative impact suggest that forest managers should prevent new fish introductions and eradicate fish from already-occupied ponds whenever possible. When fish eradication is not possible, creation of new permanent fish-free ponds nearby fish-occupied ponds may be an alternative strategy.

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Supporting Information

Table S1. Model selection results for analysis of the species occurrence and species richness. All models with AIC_c weight ≥90% are shown, as well as the two highest ranked models at each spatial scale. For each response variable is presented the model description, the number of estimable parameters (K), the sample-size adjusted AIC (AIC_c), Akaike differences (ΔAIC_c), Akaike weights and the log-likelihood (logLik), the marginal and conditional R^2 (following [69]). In bold are the covariates which confidence intervals do not overlap zero. All models have the covariate subset added as a random variable.

Response variable	Scale	Model	k	AIC_c	ΔAIC_c	Akaike weight	logLik	R^2 marginal	R^2 Conditional
Pleurodeles waltl									
	Combined	**FISH+NPW+NEPH+NPOND+NEPH:NPOND +AGRIC1000**	8	79.7	0.00	0.60	-30.96	0.68	0.68
	Combined	**FISH+NPW+NEPH+NPOND**+NTEMP+**NEPH:NPOND+AGRIC1000**	9	80.8	1.07	0.35	-30.25		
	Broad	**NPW+NEPH+NPOND**+NTEMP+**NEPH:NPOND+AGRIC1000**	8	86.6	6.88	0.02	-34.39		
	Broad	**NPW+NEPH+NPOND+NEPH:NPOND +AGRIC1000**	7	87.1	7.38	0.02	-35.86		
	Local	**FISH**+SOIL+**EMER**+FLOAT	6	89.5	9.80	0.004	-38.25		
	Local	**FISH**+EMER	4	89.8	10.10	0.004	-40.68		
	Intermediate	**NPW**+DEPH400+AGRIC400	5	96.9	17.15	0.000	-43.07		
	Intermediate	**NPW**+DTEMP400	4	97.7	17.92	0.000	-44.59		
Salamandra salamandra									
	Combined	**FISH+NEPH+EUC1000**	5	92.1	0.00	0.37	-40.67	0.54	0.60
	Combined	**FISH+NEPH+EUC400**	5	92.5	0.43	0.30	-40.88		
	Combined	**FISH+NEPH+EUC1000**+NATFOR1000	6	92.7	0.58	0.27	-39.81		
	Intermediate	**NEPH+EUC400**	4	97.7	5.58	0.02	-44.59		
	Broad	**NEPH+EUC1000**	4	98.2	6.18	0.02	-44.88		

Table S1. Cont

Response variable	Scale	Model	k	AIC_c	ΔAIC_c	Akaike weight	logLik	R^2 marginal	R^2 Conditional
	Intermediate	**NEPH**+NPOND+**EUC400**	5	98.7	6.64	0.01	-43.99		
	Broad	**NEPH**+NTEMP+**EUC1000**	5	98.8	6.71	0.01	-44.02		
	Local	**FISH+SOIL**+SUBMER	5	107.8	15.75	0.00	-48.54		
	Local	**FISH+SOIL**+HYDRO	5	108.3	16.18	0.00	-48.76		
Lissotriton boscai									
	Combined	**FISH+SUBMER+NLB+DPOND1000+DTEMP1000+EUC1000**	8	89.1	0.00	0.99	-35.66	0.64	0.64
	Broad	**NLB+DTEMP1000**	4	99.9	10.80	<0.01	-45.73		
	Broad	**NLB**+DPOND1000**+DTEMP1000**	5	100.2	11.05	<0.01	-44.73		
	Intermediate	**NLB+AGRIC400**+MONT400**+AGRIC400:MONT400**	6	102.2	13.05	<0.01	-44.58		
	Intermediate	**NLB**+NTEMP**+AGRIC400**+MONT400**+AGRIC400:MONT400**	7	102.4	12.28	<0.01	-43.51		
	Local	**FISH+SUBMER**	4	106.1	16.99	0.000	-48.82		
	Local	**FISH**+SOIL**+SUBMER**	5	106.5	17.40	0.000	-47.90		
Triturus marmoratus									
	Combined	**FISH**+FLOAT**+NTM**	5	100.9	0.00	0.38	-45.08	0.35	0.35
	Combined	**FISH**+FLOAT+EMER+NTM	6	101.9	1.05	0.22	-44.45		
	Combined	**FISH**+FLOAT+SUBMER+NTM	6	102.4	1.53	0.18	-44.69		
	Local	**FISH+FLOAT**	4	102.8	1.94	0.14	-47.17		
	Local	**FISH**+FLOAT+SUBMER	5	104.1	3.23	0.08	-46.69		
	Broad	**NTM**+AGRIC1000	4	110.8	9.92	<0.01	-51.16		
	Broad	**NTM**	3	111.4	10.49	<0.01	-52.54		

Table S1. Cont

Response variable	Scale	Model	k	AIC_c	ΔAIC_c	Akaike weight	logLik	R^2 marginal	R^2 Conditional
	Intermediate	**NTM**+DPOND400	4	112.2	11.36	<0.01	-51.88		
	Intermediate	**NTM**+AGRIC400	4	112.5	11.63	<0.01	-52.02		
Pelobates cultripes									
	Combined	**SUBMER**+SOIL+HYDRO+NTEMP**+AGRIC1000+NATFOR1000**	8	97.0	0.00	0.34	-39.57	0.53	0.53
	Combined	**SUBMER**+SOIL+HYDRO**+AGRIC1000**+NATFOR1000	7	97.1	0.12	0.32	-40.84		
	Combined	**SUBMER**+SOIL+HYDRO+DTEMP1000**+AGRIC1000+NATFOR1000**	8	98.3	1.29	0.18	-40.22		
	Local	**SUBMER+SOIL+HYDRO**	5	99.8	2.82	0.08	-44.53		
	Broad	NPOND**+AGRIC1000+NATFOR1000**	5	101.7	4.69	0.03	-45.46		
	Local	**SUBMER**+FLOAT**+SOIL+HYDRO**	6	101.8	4.79	0.03	-44.36		
	Broad	**AGRIC1000**	3	102.0	5.05	0.03	-47.87		
	Intermediate	**AGRIC400**+MONT400	4	107.1	10.10	<0.01	-49.29		
	Intermediate	**EUC400**+NATFOR400	4	107.5	10.55	<0.01	-49.52		
Hyla arborea/meridionalis									
	Combined	**SUBMER+HYDRO**+AGRIC1000+EUC1000	6	67.9	0.00	0.11		0.46	0.46
	Local	**SUBMER+HYDRO**	4	68.4	0.52	0.09			
	Local	FISH**+SUBMER+HYDRO**	5	68.5	0.67	0.08			
	Combined	FISH**+SUBMERGED+HYDROPERIOD**+AGRIC1000+EUC1000	7	68.9	1.01	0.07			
	Combined	**SUBMER+HYDRO**+AGRIC400	5	68.9	1.08	0.07			
	Combined	**HYDRO+DTEMP400**+AGRIC400	5	79.0	1.13	0.06			

Table S1. Cont

Response variable	Scale	Model	k	AIC_c	ΔAIC_c	Akaike weight	logLik	R^2 marginal	R^2 Conditional
	Local	SUBMER+FLOAT**+HYDRO**	5	69.2	1.37	0.06			
	Local	FLOAT**+HYDRO**	4	69.2	1.39	0.06			
	Combined	**SUBMER**+SOIL**+HYDRO**+AGRIC1000+EUC1000	7	69.4	1.53	0.05			
	Combined	FISH**+SUBMER+HYDRO**+AGRIC400	6	69.4	1.56	0.05			
	Combined	**SUBMER+HYDRO**+AGRIC400+AGRIC1000+EUC1000	7	69.5	1.59	0.05			
	Local	FISH+FLOAT**+HYDRO**	5	69.5	1.68	0.05			
	Local	FISH+SUBMER+FLOAT**+HYDRO**	6	69.7	1.81	0.05			
	Combined	FISH+SUBMER+FLOAT**+HYDRO**+AGRIC1000+EUC1000	7	69.8	1.92	0.04			
	Local	FISH+SUBMER+SOIL**+HYDRO**	6	70.3	2.40	0.03			
	Local	FISH**+HYDRO**	4	70.4	2.51	0.03			
	Local	**SUBMER**+SOIL**+HYDRO**	5	70.4	2.51	0.03			
	Broad	NHY+NEPH**+AGRIC1000**	5	73.2	5.31	<0.01			
	Broad	NHY**+AGRIC1000**	4	73.3	5.40	<0.01			
	Intermediate	NHY**+AGRIC400**	4	75.9	8.02	<0.01			
	Intermediate	NEPH**+EUC400**+NATFOR400	5	75.9	8.03	<0.01			
Species richness									
	Combined	FISH+NEPH+AGRIC100	5	343.5	0.00	0.06	-166.36	0	$1.25e^{-07}$
	Local	FISH+NEPH	4	343.5	0.07	0.06	-167.52		
	Local	**FISH**	3	343.6	0.15	0.06	-168.66		
	Combined	**FISH**+AGRIC100	5	343.9	0.46	0.05	-166.59		

Table S1. Cont

Response variable	Scale	Model	k	AIC_c	ΔAIC_c	Akaike weight	logLik	R^2 marginal	R^2 Conditional
	Combined	FISH+NEPH+AGRIC400	4	344.1	0.62	0.05	-167.80		
	Combined	**FISH**+AGRIC1000	4	344.2	0.75	0.04	-167.86		
	Local	**FISH**+HYDRO	5	344.3	0.82	0.04	-166.77		
	Local	**FISH**+NEPH+HYDRO	4	344.3	0.87	0.04	-167.92		
	Local	**FISH**+FLOAT	5	344.3	0.88	0.04	-166.80		
	Combined	FISH+NEPH+EUC1000	6	344.5	1.03	0.04	-165.73		
	Combined	FISH+NEPH+EUC1000+NATFOR1000	5	344.5	1.08	0.04	-166.90		
	Combined	FISH+FLOAT+NEPH	4	344.6	1.14	0.04	-168.06		
	Broad	NEPH+AGRIC1000	5	344.7	1.22	0.03	-166.97		
	Combined	FISH+NEPH+NPOND	3	344.8	1.39	0.03	-169.28		
	Intermediate	NEPH	4	344.8	1.39	0.03	-168.18		
	Broad	FISH+NPOND	5	344.9	1.41	0.03	-167.07		
	Combined	FISH+NEPH+MONT1000	6	344.9	1.44	0.03	-165.93		
	Combined	FISH+NEPH+NPOND+AGRIC1000	5	344.9	1.47	0.03	-167.09		
	Combined	FISH+NEPH+EUC400	4	345.0	1.50	0.03	-168.24		
	Combined	**FISH**+NATFOR400	4	345.0	1.56	0.03	-168.27		
	Combined	**FISH**+EUC1000	6	345.0	1.59	0.03	-166.001		
	Combined	FISH+NEPH+AGRIC1000+NATFOR1000	6	345.1	1.67	0.03	-166.04		
	Combined	FISH+NEPH+AGRIC1000+MONT1000	5	345.2	1.73	0.03	-167.23		
	Combined	FISH+NEPH+NATFOR1000	5	345.2	1.76	0.03	-167.24		

Table S1. Cont

Response variable	Scale	Model	k	AIC_c	ΔAIC_c	Akaike weight	logLik	R^2 marginal	R^2 Conditional
	Combined	**FISH**+FLOAT+HYDRO	5	345.4	1.90	0.02	-167.31		
	Broad	**NEPH**+EUC1000+NATFOR1000	5	345.4	1.93	0.02	-167.33		
	Combined	FISH+NEPH+MONT400	5	345.4	1.94	0.02	-167.33		
	Intermediate	NEPH+NPOND	4	345.4	1.98	0.02	-168.48		

FISH - presence of predator fish (FISH); HYDRO – hydroperiod; SOIL - soil type (muddy or shale); FLOAT - % of floating aquatic vegetation; EMER - % of emergent aquatic vegetation; SUBMER - % of submersed aquatic vegetation; and the percentage of aquatic vegetation; Proportion of land cover(AGRIC –agriculture; EUC – eucalypt plantations; MONT – montados; NATFOR – native forest); NEPH - the distance to the nearest ephemeral waterlines (m); NTEMP - the distance to the nearest temporary waterlines (m); NPOND – distance to ponds (m); DEPH – density of ephemeral waterlines (intermediate scale number per 50 ha; broad scale: number per 314 ha); DTEMP - density of temporary waterlines (intermediate scale number per 50 ha; broad scale: number per 314 ha); DPOND - density of ponds (intermediate scale number per 50 ha; broad scale: number per 314 ha); NPW – distance to nearest occupied pond with *Pleurodeles waltl* (m); NSS - distance to nearest occupied pond with *Salamandra salamandra* (m); NLB– distance to nearest occupied pond with *Lissotriton boscai* (m); NTM – distance to nearest occupied pond with *Triturus marmoratus* (m); NPC – distance to nearest occupied pond with *Pelobates cultripes* (m); NHY – distance to nearest occupied pond with *Hyla* spp. (m)).

CHAPTER 3

EFFECTS OF EXOTIC EUCALYPT PLANTATIONS ON NATIVE BATS IN A MEDITERRANEAN LANDSCAPE

Preface

It is well-studied how forest structure and composition affects bat habitat quality by influencing the availability and accessibility of roosts and prey (Hayes & Loeb, 2007), predator avoidance (Baxter et al., 2006) and animal movement (Jung et al., 2012). Physical clutter is likely to influence bat flight and make it more difficult to accurately detect and capture prey due to background echoes (Brigham et al., 1997). Stand clutter may be more important than prey availability in determining habitat use by fast-flying bats (Armitage & Ober, 2012; Grindal, 1996). Very dense clutter, even with greater insect abundance, has been shown to affect both capture success and capture time, making these areas also unsuitable for gleaning and hawking species (Adams et al., 2009; Rainho et al., 2010; Smith & Gehrt, 2010; Titchenell et al., 2011; Webala et al., 2011). In Australia, the impact of eucalypt plantations and use of different age stands by bats have been thoroughly studied (e.g. Hobbs et al., 2003; Law et al., 2011), however, despite its widespread use as a plantation tree little equivalent research has been done outside the native range of eucalypts, even in biodiversity hotspot areas such as the Mediterranean basin (Goiti et al., 2008).

In this Chapter, I compared the overall bat activity, species richness and Kuhl's bat *Pipistrellus kuhlii* (the most abundant bat species in the study area) activity between eucalypt plantations and native *montado* habitat, in 1 km transects using a bat detector and examined the influence of stand, landscape and survey variables within plantations on the response variables. I applied a zero-inflated Poisson generalised linear mixed model to a set of predictor variables that included eleven plantation stands, three landscape and two survey variables. This study provides the first evaluation of the impact of eucalypt plantations, considering different age stands, on bat activity in the Mediterranean basin and suggests forest management guidelines to promote this guild.

This Chapter is written in the style of and will be submitted to the journal "Conservation Biology".

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Effects of exotic eucalypt plantations on native bats in a Mediterranean landscape

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ABSTRACT

The transformation of native habitats into forest plantations for industrial purposes frequently has negative consequences for biodiversity. We evaluated the impact of eucalypt plantations on native bats in the Mediterranean area, taking Portugal as a case study. We compared the overall bat activity, species richness and Kuhl's bat *Pipistrellus kuhlii* (the most abundant bat species in the area) activity between eucalypt plantations and native *montado* habitat, and examined the influence of stand, landscape and survey variables within plantations on the response variables. A set of eleven plantation stands, three landscape and two survey variables were employed as predictor variables using a zero-inflated Poisson generalised linear mixed model. Hawking and generalist bats of the genus *Pipistrellus* were the most frequently detected species. Bat activity, species richness and *Pipistrellus kuhlii* activity were higher in native *montado* than in any of the eucalypt stands. Mature eucalypt plantations showed the highest bat activity, while clear-cut areas showed the

lowest. Generally, within eucalypt stands, complex high-level vegetation structure, from the ground level up to 3 metres high, and proximity to water points were associated with higher levels of bat and *P. kuhlii* activity, and species richness. The results suggest that in order to promote bat diversity and activity in exotic eucalypt plantations in the Mediterranean region, it is important to provide a high density of water points, maintain plots of mature plantations, and promote understorey clutter.

Keywords: *Eucalyptus* plantations; forest clutter; forest management; Mediterranean region; non-native trees; *Pipistrellus*

1. Introduction

Habitat change and degradation have been identified as important anthropogenic drivers of biodiversity loss (Millenium Ecosystem Assessment, 2005). Forest plantations provide an example of this change over recent decades, and since 2005, the planted area worldwide has increased by almost 5 million hectares every year, reaching a total 264 million hectares in 2010 (FAO, 2010). These plantations are often considered as "ecological deserts" (Gardner et al., 2007), since they are mostly composed of monocultures of exotic species managed intensively for timber production (Gardner et al., 2007; Kanowski et al., 2005). One of the most planted tree in the world is the eucalypt (*Eucalyptus* spp.) (FAO, 2010), representing 8% of planted forests over 20 million hectares globally (Laclau et al., 2013).

Eucalypt plantations are highly controversial and so are the results of the impact they have on the ecosystem, being usually associated with soil water and nutrients depletion, erosion promotion and loss of biodiversity (Turnbull, 1999; Vacca et al., 2000).

Bats play an important role in the food web (Hutson et al., 2001; Kunz et al., 2011) and are often considered to be good bioindicators for the wider ecosystem (Jones et al., 2009). Approximately 25% of European bats are threatened (Temple and Terry, 2009), principally due to habitat destruction and modification as well as roost site disturbance (Hutson et al., 2001). The impact of eucalypt plantations on bats has been studied in Australia (e.g. Hobbs et al., 2003; Law et al., 2011), but little

equivalent research has been done outside the native range of eucalypts, even in biodiversity hotspot areas such as the Mediterranean basin (Goiti et al., 2008), despite its widespread use as a plantation tree. In Portugal, especially, the forest product industry occupies an important position in the economy, with timber products valued at over 2.2 billion euros in 2011, most of this derived from eucalypt plantations (CELPA, 2012). Forest covers 35% of mainland Portugal, and more than a quarter of this area is dominated by eucalypt (26%), and both Maritime pine (*Pinus pinaster*) and native cork oak (*Quercus suber*) occupy 23% each (ICNF, 2013). Given the significance of the Mediterranean region for native biodiversity (Brooks et al., 2002) and the predominance of eucalypt on forest cover, there is an urgent need to evaluate the impact of these plantations on native biodiversity and develop management practices within these plantations that are more compatible with biodiversity.

The main objectives of this study were: (i) to evaluate the impact of eucalypt plantations on bat species richness and the activity, focusing on activity patterns of the dominant species in the community, Kuhl's bat *Pipistrellus kuhlii*, and (ii) to determine the ecological factors affecting bat activity within eucalypt plantations, with a specific emphasis on stand structure. The results will help inform the development of management practices to enhance biodiversity in these widespread productive landscapes.

2. Materials and methods

2.1. Study area

We carried out the study in central-east Portugal, Castelo Branco district (39º40' – 40º10'N, 7º0' – 7º35'W). The area has a Mediterranean climate and the forest land cover is dominated by Maritime pine tree (50%), eucalypt plantations (*Eucalyptus globulus*) with different age stands (28%), cork oak and Holm oak (*Quercus ilex*) forest and *montados* (oak savannah-like woodland) (both 9% each). In addition to forestry, the landscape is used patchily for livestock grazing, olive (*Olea europaea*) groves, wheat (*Triticum* spp.) production, and scrubland areas dominated by *Cytisus* spp., *Cistus* spp. and *Erica* spp. (Fig. 1).

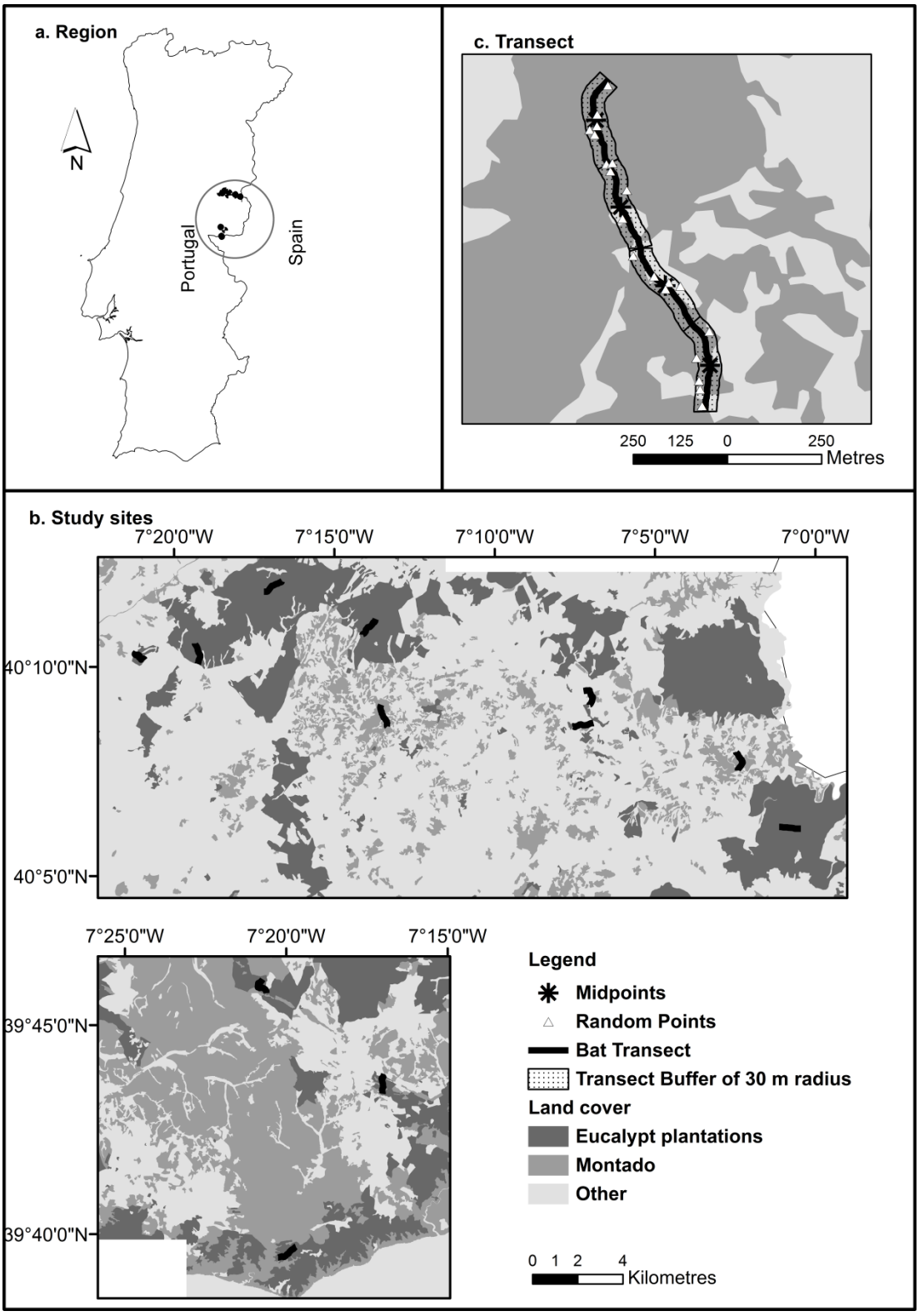

Fig. 1. (a) and (b) Map of the study area, showing the distribution of bat transects and the two major land cover types, *montado* and eucalypt stands; and (c) schematic representation of a 1 km bat transect in a *montado*, showing the 30 m buffer each side of the transect and its division into 4 equal-sized plots, each one with a midpoint, and the visualization of the random points used to assess eleven plantation stand variables.

The *montados* in the study area are actively exploited, with cattle grazing and cork extraction. Most eucalypt plantations are on their third rotation, planted for the first time in the mid-1970s, and three types of plantation can be recognized according to the stand age: clear-cut areas (1-1.5 years); young stands (3-6 years post-clear cutting); and mature stands (12-16 years post-clear cutting). The mature stands represent the optimal harvest age for eucalypts in Portugal for the pulp and paper industry.

2.2. Sampling methodology

We located thirteen 1 km transects along dirt forest roads in four land cover types: cork and Holm oak *montado*, clear-cut areas, young and mature eucalypt stands (Fig. 1 a and b).

We used three replicate transects in each land cover type, with the exception of mature plantations, where we placed four transects. We sampled seven transects monthly between July-September 2010 and March-September 2011, and we sampled the remaining six transects monthly between August-September 2010 and March-September 2011. We walked the transects at a constant pace along dirt roads, between four to five metres wide, which cross the forest plantations and *montados*. The number of transects and the survey frequency adopted have been followed by several authors (Berthinussen and Altringham, 2011; Hale et al., 2012; Jung et al., 2012; Rainho, 2007). Previous studies around Europe have shown that while commuting, bats exhibit great variation in distance covered, ranging from 0.6 km for *P. pipistrellus* (Nicholls and Racey, 2006), to around 13 km for *Nyctalus leisleri* (Shiel et al., 1999) and up to 41 km for *Eptesicus serotinus* (Robinson and Stebbings, 1997). Since the focal species for activity patterns in our study was the Kuhl's pipistrelle *P. kuhlii*, we separated transects spatially by at least 1 km, to minimise spatial auto-correlation. However, this may not be sufficient spatial separation in relation to some of the other species encountered, so we undertook further specific analysis for spatial auto-correlation using spline correlogram plots (Zuur et al., 2009). We removed one of the transects in mature stands prior to data analysis since

it was located 300 metres away from a roost area, and hence the results for this transect were biased by bats leaving the roosts shortly after sunset.

2.3 Bat sampling

Transect surveys started at civil twilight after sunset and lasted for three hours, therefore up to three transects were made per night. The order in which the transect surveys were done changed each month to cover all time periods surveyed. We assessed bat activity, quantified by bat passes, using a 10x time expansion ultrasonic bat detector (Petterson D-240x, Pettersson Elektronik AB, Uppsala, Sweden), connected to a digital recorder (R-09, Edirol, Roland Corporation, Shizouka, Japan), and located these using a GPS (Garmin eTrex Vista, Garmin, Southampton, United Kingdom). We defined a bat pass as a sequence of two or more echolocation pulses in the 17 second recording. We did not use buzz feedings as a sign of bat activity because they were very scarce throughout the surveys. We recorded relevant weather variables (temperature and humidity) using a pocket weather meter (Kestrel® 3000, Nielsen Kellerman, Boothwyn, USA), and the time since civil twilight. We did not sample on nights with rain, strong winds or with conditions adverse to bat activity (Russo and Jones, 2003).

We saved bat activity data files in WAV format (sampling rate at 44.1 kHz and 16 bits/sample) and analysed them with sound analysis software (BATSOUND PRO v. 3.331b; Pettersson Elektronik AB, Uppsala, Sweden) using a 512 point fast Fourier transform with Hamming window for spectrogram analysis (Rebelo and Jones, 2010). Call parameters were measured using crosshair screen cursors, temporal variables (duration and inter-pulse interval) were measured from oscillograms, and frequencies (highest, lowest and frequency of peak energy) were taken from power spectra (Rebelo and Jones, 2010). We identified species or genera using Ahlén and Baagøe, (1999); Russo and Jones, (2002) and Rainho et al., (2011). Although this is a fast, low-cost method to identify bats, there are constraints that have to be acknowledged. Echolocation detectability varies with climatic conditions (e.g. detectability decreases as relative humidity increases), with the sound amplitude of each species calls (this varies from as low as 50dB to ca. 110dB), with the frequency

of the calls (higher echolocation frequencies suffer a higher attenuation in the atmosphere and hence are detectable over a shorter distance) and with vegetation clutter (e.g. dense vegetation can cause bats to produce fewer diagnostic calls) (Broders et al., 2004). Additionally, some bat species cannot be identified accurately using the method described above because of similar echolocation characteristics, in which case we considered the species complex. That is the case for *Nyctalus lasiopterus* and *N. noctula*, *Eptesicus serotinus* and *E. isabellinus*, *Myotis myotis* and *M. blythii*, *M. emarginatus* and *M. bechsteinii* and for *P. pygmaeus* and *Miniopterus schreibersii*. There is also some overlap on the frequency ranges of *P. kuhlii* and *P. pipistrellus*, so when this overlap was identified, all calls were classified as *Pipistrellus* spp. In certain conditions – bats flying in open habitat, avoiding obstacles – it might be possible that echolocation characteristics of *Eptesicus* and *N. leisleri* may overlap. In these situations we analysed discriminatory characters of the calls (such as call shape, pulse duration and interval between pulses) and whenever possible distinguished between the two genera (Goerlitz et al., 2010; Jensen and Miller, 1999; Waters and Jones, 1995).

2.4 Habitat structure

To characterise habitat structure, we placed a 30 m buffer on both sides of each 1 km transect, then divided the buffered transect into four equal 250 m x 30 m plots and determined the midpoint for each of these plots (Fig. 1c). In order to sample the habitat variables, we distributed 20 random points equally amongst these four plots, five points per plot (Fig. 1c). In each of the plots, we assessed eleven plantation stand variables: land cover type; canopy; diameter at breast height; tree height; shrub and herb cover proportion; low-level understorey clutter (up to 1 metre high); high-level understorey clutter (from 1 to 3 metres high); low-level tree clutter (up to 1 metre high); high-level tree clutter (from 1 to 3 metres high); and very high-level tree clutter (more than 3 metres high). We also recorded three landscape variables: aspect, slope and distance to the nearest water point (see Supplementary material Table S1).

2.5 Data analyses

We applied the data exploration techniques described by Zuur et al., (2009) to the datasets on overall bat activity (the number of files containing bat calls) (Lentini et

al., 2012), species richness and *P. kuhlii* activity. To assess collinearity, we used the Spearman rank correlation coefficient because it makes no assumption about linearity between two variables (Zuur et al., 2009); the value ±0.6 was chosen to indicate high collinearity between variables; where high collinearity was found, the variables were not used together in the same model. This value was chosen as a compromise, since high collinearity is defined by some authors as where $|r| > 0.5$ (Zuur et al., 2009), whereas other authors propose a value of $|r| > 0.7$ (Dormann et al., 2013).

In order to determine whether there was a difference in the studied response variables between eucalypt plantation and native forest (*montado*) we applied Kruskal-Wallis tests followed by a post-hoc Kruskal-Wallis procedure using the R-package pgirmess (Giraudoux, 2012), based on the algorithm described in Siegel and Castellan, (1988). Further analysis (Kruskal-Wallis tests and modelling) were only applied to eucalypt plantations and the impact of the plantation structure on bat activity and species richness. To assess which predictors better explained the behaviour of the response variables, we used generalised linear mixed models (GLMM) with a zero inflated Poisson distribution and a log link function (due to the excess number of zeros in our data) fitted using the Laplace approximation to the deviance. We applied a three-step approach to determine the best top-ranked models. Firstly, we combined all valid combinations, avoiding multicollinearity, making a total of eight global models. Secondly, we used data dredge statistics (dredge—MuMIn R package) (Barton, 2012) to run GLMM on those models. Thirdly, we used an information-theoretic approach to select the best model for the overall bat activity, species richness and *P. kuhlii* activity (Burnham and Anderson, 1998). We used the Akaike's information criterion corrected for small sample sizes (AIC_c) in R-package glmmADMB (Skaug et al., 2012) to rank models with $\Delta\ AIC_c$ lower than 2 (Burnham and Anderson, 1998). If one model had an Akaike weight of more than 90%, it was considered as the most parsimonious model of all tested models. Otherwise, we calculated model-averaged estimates and unconditional 95% confidence intervals with multimodel inference (Burnham and Anderson, 1998). Confidence intervals of the explanatory variables that overlapped zero were considered not statistically significant, so they were not considered for further analyses. The relative importance of each variable (rank) was determined by summing the weights for every model where that variable

was present (Burnham and Anderson, 1998). We plotted the variables that were determined to influence the response variables. Model validation was calculated by applying a series of 50 10-fold cross-validations (Koper and Manseau, 2009).

We assessed spatial auto-correlation by constructing spline correlograms of the Pearson residuals (Bjørnstad and Falck, 2001), produced for the top-ranked models for each response variable, using R-package ncf (Bjørnstad, 2009). One of the spline correlograms was to assess spatial auto-correlation within the transect, with a lag interval of 1 km, and the other used a lag interval of 5 km to evaluate the correlation of transects situated within a radius of 5 km.

In order to evaluate the effect size of each predictor variable, we calculated the odds ratio using the multi-average models for each response variable (Nakagawa and Cuthill, 2007).

3. Results

We recorded a total of 537 bat passes in 2131 min (Table 1). Thirteen bat species or species complexes were detected, with the most frequent being from the *Pipistrellus* genus (*P. kuhlii*, followed by *P. pygmaeus*/*Miniopterus schreibersii* and *P. pipistrellus*), which together comprised more than 80% of all bat passes (Table 1). Passes of *Eptesicus serotinus*/*isabellinus* and *Nyctalus leisleri* were recorded less than 20 times each, while other detected species (*Barbastella barbastellus*, *Tadarida teniotis*, *Nyctalus lasiopterus*/*noctula*, *Plecotus* spp., *Myotis myotis*/*blythii*, *M. escalerai*, *Hypsugo savii* or *Myotis emarginatus*/*bechsteinii*) were recorded less than ten times each.

The highest number of bat passes was recorded in *montado*, followed by mature eucalypt plantations, while the lowest number was in clear-cut areas (Table 1). The number of bat species was highest in *montado* and mature eucalypt plantations, each having ten species recorded. Most of the species were common to both of these land cover types. The exceptions were *Hypsugo savii*, which was not recorded in mature eucalypt plantations, and *Myotis escalerai*, which was not recorded in *montado*.

Overall bat activity (Kruskal-Wallis, $\chi^2 = 57.93$, $P<0.001$), species richness (Kruskal-Wallis, $\chi^2 = 55.11$, $P<0.001$) and *P. kuhlii* activity (Kruskal-Wallis, $\chi^2 = 54.06$, $P<0.001$) were significantly different between *montados* and eucalypt plantations (Table S2). Within the eucalypt age stands, there were significant differences ($P<0.001$) among medians of the habitat structure variables (canopy, diameter at breast height, tree height, shrub and herb cover proportion, high-level understorey clutter (from 1 to 3 metres high), high-level tree clutter (from 1 to 3 metres high) and very high-level tree clutter (more than 3 metres high) and distance to the nearest water point) as well as among site variables (aspect and slope) (Table S2). Only two variables, relating to low-level understorey clutter (up to 1 metre high) and low-level tree clutter (up to 1 metre high), did not show a significant difference ($P>0.001$).

The cross-validation results were in line with the ΔAIC_c analysis below, with identical ranking of models based on mean squared error. The predictive performance was acceptable, with root mean squared error for all models and response variables being smaller than the standard deviation. For the chosen models, there was no positive spatial auto-correlation detected within transects (1 km) or between transects that were located less than 5 km apart.

There was no single best model to explain variations in any of the response variables (Table S3). Distance to the nearest water point, temperature, tree height, high-level tree clutter all ranked high in relative importance in all averaged models of bat and *P. kuhlii* activity and species richness while low-level understorey clutter stood out only for the bat activity and species richness models (Table 2).

Table 1

Recorded bat activity categorised by species recorded and by land cover (mature, young and clear-cut eucalypt stands, and *montado*), the absolute number of bat passes (mean ± standard deviation) and the relative number (bat passes divided by 30 minutes for each land cover), and species richness per land cover.

	Total bat passes				
	Mature	Young	Clear-cut	*Montado*	Total
Myotis emarginatus/bechsteinii	1			1	2
Myotis myotis/blythii	2			5	7
Myotis escalerai	1	3			4
Myotis spp.	3	1		6	10
Pipistrellus pipistrellus	19	7	5	28	59
Pipistrellus kuhlii	69	38	20	155	282
Pipistrellus pygmaeus/ Miniopterus schreibersii	26	10	1	41	78
Pipistrellus spp.	12	6	3	16	37
Hypsugo savii				1	1
Nyctalus leisleri	5	3		11	19
Nyctalus lasiopterus/noctula	3		1	1	5
Eptesicus serotinus/isabellinus	5	2	1	4	12
Barbastella barbastellus		2			2
Plecotus spp.			1		1
Tadarida teniotis	2			3	5
Unidentified	3	2	1	7	13
Relative number (N/30 min)	6.9	4.7	2.1	15.4	7.3
Absolute number	151	74	33	279	537
mean±SD	1.02±2.04	0.64±1.17	0.28±0.64	2.4±7.70	
Species richness	10	7	6	10	13

Table 2

Model averaged coefficients for the variables of the top-ranked models (Akaike's weight ≥ 90%) for overall bat activity, species richness and *Pipistrellus kuhlii* activity, the confidence intervals and the relative importance of the variables, odds ratio and confidence interval at 95% level. (* p<0.05; **p<0.01; ***p<0.001)

Response variable	Predictor	Model averaged coefficient±SE	Confidence Intervals		Importance	Odds ratio (CI 95%)
			2.5%	97.5%		
Bat activity	Intercept	-1.63±0.77*	-3.16	-0.11		0.19 (0.04-0.89)
	High-level tree clutter	1.47±0.49**	0.51	2.43	1	4.34 (1.67-11.30)
	Low-level understorey clutter	1.67±0.56**	0.56	2.75	0.84	5.29 (1.74-16.06)
	CT	-0.16*±0.07*	-0.30	-0.03	1	0.85(0.74-0.97)
	NW	-0.0016±0.00035***	-0.0023	-0.00089	1	0.99 (0.99-1.00)
	Slope	-0.06±0.03*	-0.11	-0.01	1	0.94 (0.89-0.99)
	T	0.04±0.01**	0.0091	0.06	0.93	1.04 (1.01-1.07)
	TH	0.16±0.04***	0.08	0.24	0.97	1.18 (1.09-1.28)
	SC	-0.01±0.01	-0.03	0.01	0.33	0.99 (0.97-1.01)
	Low-level tree clutter	1.42±0.50**	0.44	2.39	0.16	4.13 (1.56-10.94)
	DBH	0.05±0.01***	0.02	0.07	0.03	1.05 (1.02-1.07)
Species Richness	Intercept	-2.39±0.67***	-3.71	-1.08		0.09 (0.02-0.34)
	High-level tree clutter	0.99±0.43*	0.14	1.85	1	2.71 (1.16-6.36)
	Low-level understorey clutter	1.05±0.47*	0.13	1.97	0.64	2.85 (1.13-7.16)
	NW	-0.002±0.0003***	-0.002	-0.0009	1	0.99 (0.99-1.00)

Table 2

Cont.

Response variable	Predictor	Model averaged coefficient±SE	Confidence Intervals		Importance	Odds ratio (CI 95%)
			2.5%	97.5%		
	Slope	-0.03±0.02	-0.08	0.01	0.34	0.97 (0.92-1.01)
	T	0.04±0.02*	0.005	0.07	1	1.04 (1.01-1.07)
	TH	0.12±0.03***	0.05	0.18	0.92	1.12 (1.05-1.20)
	CT	-0.09±0.07	-0.23	0.05	0.31	0.91 (0.79-1.05)
	Low-level tree clutter	0.99±0.47*	0.07	1.91	0.34	2.69 (1.08-6.73)
	High-level understorey clutter	0.01±0.01	-0.01	0.04	0.13	1.01 (0.98-1.04)
	Aspect	-0.00057±0.001	-0.003	0.002	0.04	0.99 (0.99-1.00)
	HC	0.44±1.06	-1.63	2.52	0.07	1.56 (0.19-12.44)
	SC	-0.003±0.01	-0.022	0.02	0.04	0.99 (0.98-1.02)
	DBH	0.03±0.01*	0.003	0.05	0.08	1.03 (1.00-1.05)
Pipistrellus kuhlii activity	Intercept	-2.61±1.28*	-5.12	-0.09		0.07 (0.01-0.91)
	High-level tree clutter	1.93±0.74**	0.47	3.38	0.99	6.87 (1.60-29.49)
	NW	-0.003±0.0006***	-0.004	-0.002	1	0.99 (0.99-1.00)
	T	0.07±0.02**	0.03	0.11	1	1.07 (1.03-1.12)
	Low-level understorey clutter	1.54±0.84	-0.11	3.18	0.62	4.66 (0.90-24.18)
	TH	0.13±0.06*	0.02	0.24	0.65	1.14 (1.02-1.27)
	Slope	-0.08±0.05	-0.17	0.01	0.53	0.92 (0.85-1.019

Table 2

Cont.

Response variable	Predictor	Model averaged coefficient±SE	Confidence Intervals		Importance	Odds ratio (CI 95%)
			2.5%	97.5%		
	HC	-2.64±1.64	-5.88	0.59	0.68	0.07 (0.003-1.81)
	Aspect	0.0031±0.002	-0.001	0.007	0.47	1.00 (0.99-1.01)
	CT	-0.11±0.10	-0.31	0.09	0.22	0.90 (0.73-1.10)
	DBH	0.03±0.02	-0.001	0.06	0.19	1.03 (0.99-1.07)
	Low-level tree clutter	1.03±0.74	-0.43	2.49	0.06	2.79 (0.65-12.09)
	High-level understorey clutter	0.03±0.02	-0.009	0.06	0.25	1.03 (0.99-1.07)
	SC	-0.01±0.01	-0.04	0.02	0.08	0.99 (0.96-1.02)
	Canopy	-1.45±1.30	-4.001	1.12	0.03	0.23 (0.02-3.06)

For bat activity, six models had $\Delta AIC_c \leq 6$, which accounted for 90% of the AIC_c weights among the candidate models analysed (Table S3), illustrating the uncertainty of the selected models. Survey-related parameters (temperature and time since civil twilight) had opposite effects on bat activity, positive and negative, respectively (Table 2). Habitat structure variables (high-level tree clutter, low-level understorey clutter and tree height) had a positive influence on this response variable, and all ranked high (rank > 0.80) for the relative importance of the variables of the averaged model (Table 2). Slope was negatively correlated with bat activity, the more steep it was the less bat activity was recorded (Table 2). An increase from 40 to 60% of low-level understorey clutter and high-level tree clutter raised bat activity by 39% and 36%, respectively (Fig. 2). Even more evident was the effect of tree height: bat activity increased was 1.3 times greater in mature stands (10 metres high) than in young stands (5 metres high) (Fig. 2). It was also evident that the proximity of water played an important role, with bat activity 33% lower in sites where ponds were 500 m distant compared with sites where ponds were within 250 m.

For species richness, there were 19 models with $\Delta AIC_c \leq 4.41$, comprising 90% of the AIC_c weight of the candidate models (Table 2 and S3), once more highlighting the uncertainty of the top ranked models. Temperature and distance to the nearest water point were the most relevant predictors of species richness, along with positive effects of tree height and high-level tree clutter (Table 2 and Table S4). All of these variables ranked high in importance (Table 2). Lower-ranked, but still with a positive influence on species richness, were low-level understorey clutter (rank = 0.64) and low-level tree clutter (rank = 0.34) (Table 2). Species richness declined by 66% between sites with a pond within 250 metres and sites with a pond 500 metres away. Tree height had the greatest impact on species richness, which was 73% higher in mature stands than young ones (Fig. 2). An increase in high-level tree clutter from 40-60% led to a 22% increase in species richness, and a similar increase in low-level understorey clutter led to a 23% increase in species richness (Fig. 2). Low-level tree clutter increased species richness by 22% (Fig. 2). Again, the importance of water was evident, with species richness 33% lower in sites with a pond 500 metres distant compared with sites with a pond within 250 metres (Fig. 2).

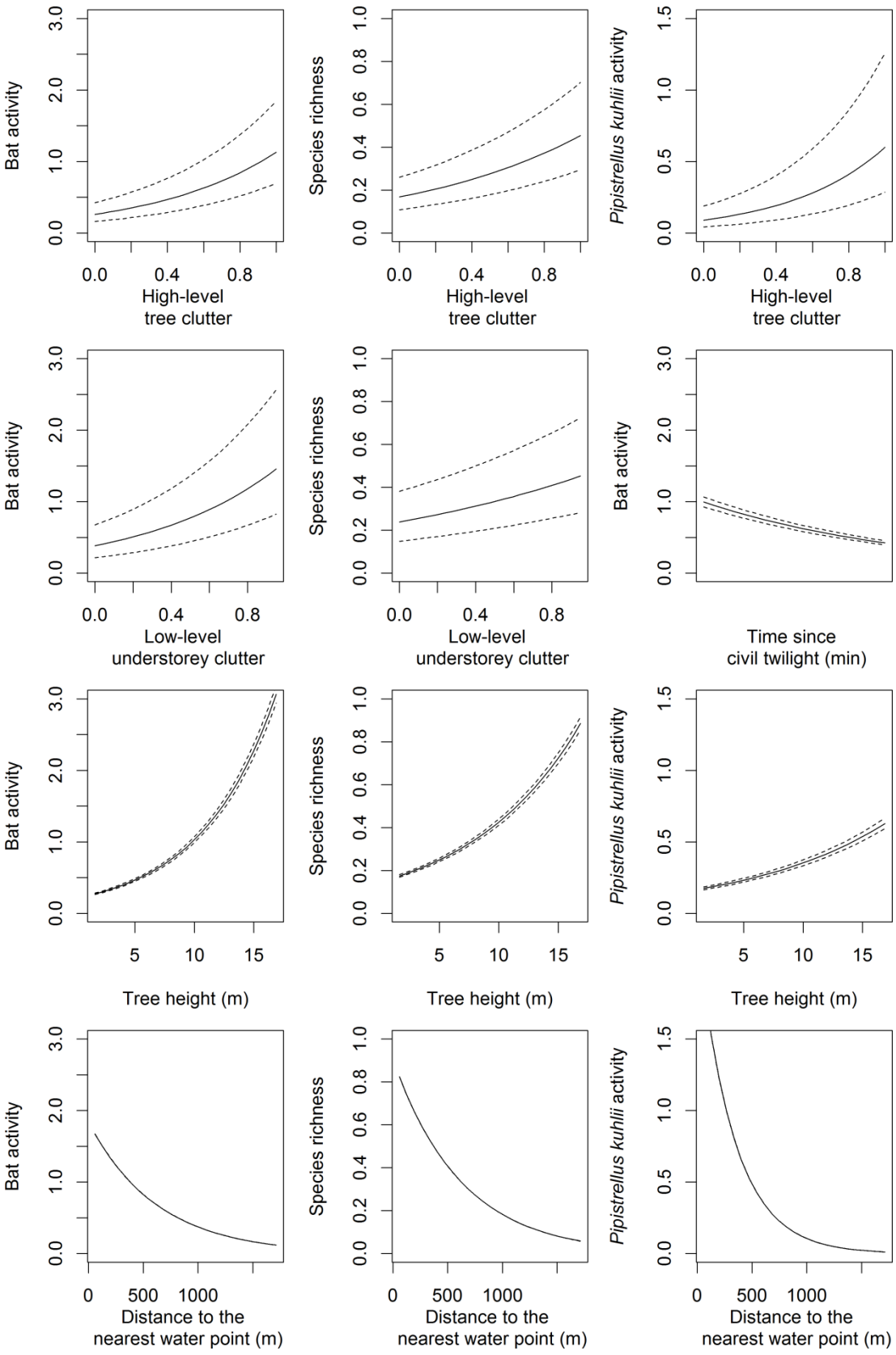

Fig. 2. Fitted values predicted by the averaged models for each of the response variables (bat activity, species richness and *P. kuhlii* activity). The dashed line is the confidence interval at 95%.

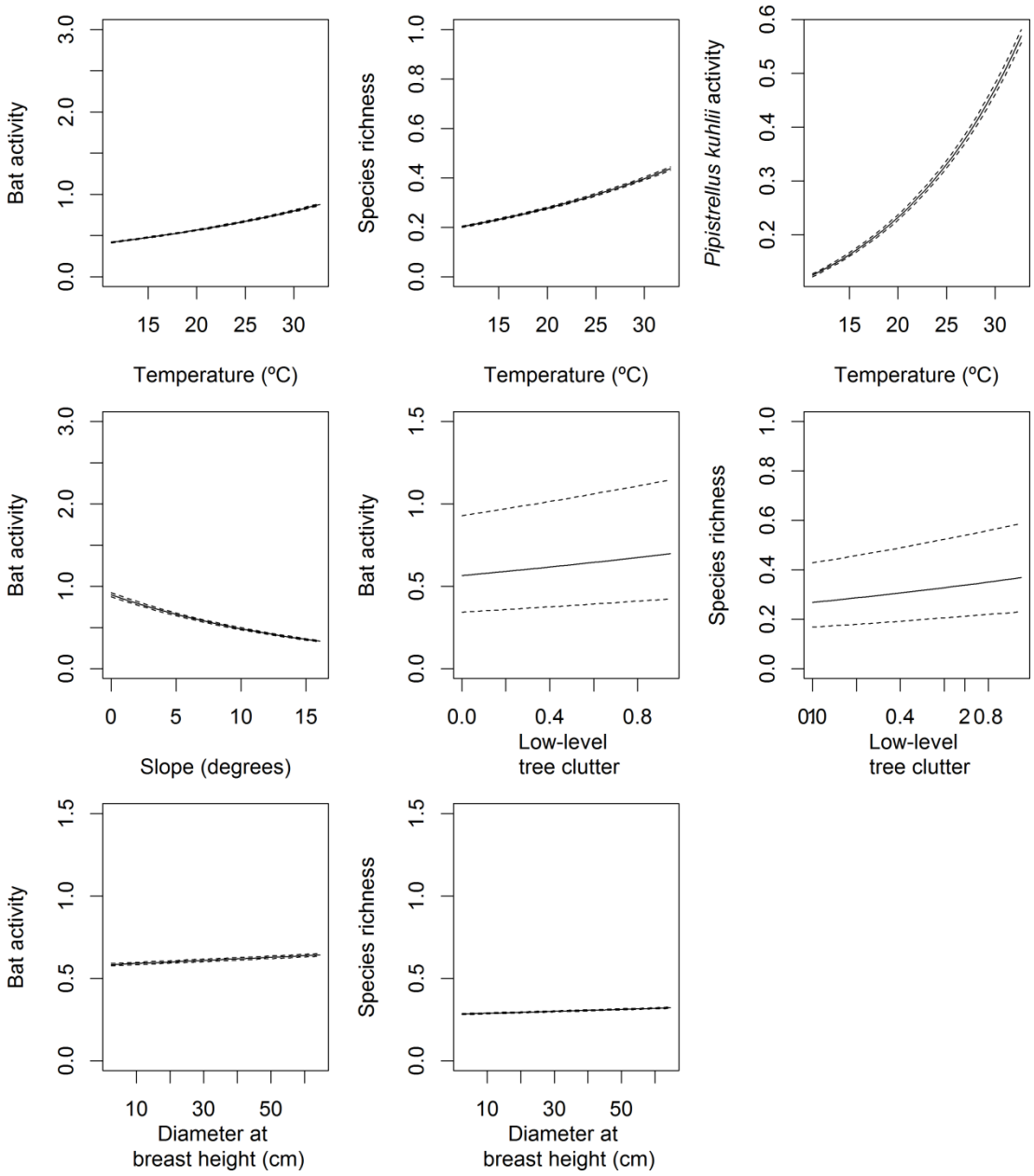

Fig. 2. Cont.

For *P. kuhlii* activity, there were 45 top-ranked models with an AIC_c weight of 90%, with a $\Delta AIC_c \leq 3.45$ (Table 2 and Table S3), again with high uncertainty. For the averaged model, the most important variables were once more temperature, distance to nearest water point, and high-level tree clutter, all ranked high in terms of relative importance (Table 2). The next most influential variable was tree height, with a relative importance of 0.65. *P. kuhlii* activity showed the greatest relative response, being 52% lower in sites with a pond 500 metres distant compared with sites with a pond within 250 metres (Fig. 2). An increase of 40% of high-level tree clutter

resulted in increases in *P. kuhlii* activity of 51% (Fig. 2). Stands of 10 metres height had 80% had twice more *P. kuhlii* activity than stands 5 metres high (Fig. 2).

4. Discussion

Our results demonstrated that native *montados* are of greater importance for bat populations than exotic eucalypt plantations. *Montados*, with low-intensity cattle grazing and sparse understorey vegetation, are associated with a high abundance of insects, especially from the families of Hymenoptera and Coleoptera (Mendes et al., 2011). Some of the *Pipistrellus* species prey upon these insect families (*P. kuhlii* (Goiti et al., 2003), *P. pipistrellus* and *P. pygmaeus* (Bartonička et al., 2008)). In eucalypt plantations, insect abundance and diversity are low compared with traditional land cover, like *montado* (Zahn et al., 2009). Low plant diversity also results in low bat activity, which is a consequence of intensive stand establishment techniques (Lomba et al., 2011; Wen et al., 2010), resulting in water depletion (Mendham et al., 2011), soil erosion (Vacca et al., 2000), and release of allelopathic chemicals into the soil inhibiting the germination of certain plants (Zhang et al., 2010). The decreased bat activity associated with eucalypt plantations and the preference for *montados* and riparian habitats has been described for the Mediterranean region (Di Salvo et al., 2010; Rainho, 2007). Nevertheless, when the surrounding habitat is of poor quality, bats may forage or roost in eucalypt plantations. In the Basque Country, Spain, *Rinolophus euryale* selected positively deciduous forests and eucalypt plantations to forage, while avoiding pine plantations (Aihartza et al., 2003). The authors believed that the reason for this particular behaviour might had been correlated with the use of pesticides in the pine plantations, decreasing prey availability. Also in Spain, Flaquer et al., (2009) described the use of scattered eucalypt trees as roosting sites for *Pipistrellus nathusii*, when the surrounding landscape was openland.

Despite the overall greater importance of *montados* for bats compared with eucalypt plantations, the management of these plantations may have a significant effect on the local bat community. Within eucalypt stands, complex high-level vegetation structure and proximity to water points were associated with high levels of bat and *P. kuhlii* activity, and species richness. Water sources have long been recognised as important for bats (e.g. Flaquer et al., 2009; Lisón and Calvo, 2013), either directly

in areas of water scarcity, or indirectly because they create foraging opportunities for bats through associated insects. In the Mediterranean region, bats can lose nearly 30% of their body weight when active (Lisón and Calvo, 2011), so access to water and associated food sources is likely to be particularly important. The highest number of bats and *P. kuhlii* activity in our study were recorded in mature plantations. Older stands are quite often favoured as roost sites due to a micro-climate with more stable temperature and reduced clutter compared with younger stands (Crampton and Barclay 1998; Humes et al. 1999; Perry et al. 2007), but also as foraging areas with higher insect abundance (Borkin and Parsons 2011). Overall, however, our results showed a positive association of *P. kuhlii* activity with tree clutter, from the ground level up to 3 metres high. Tree and understorey clutter were observed for bat activity and species richness, especially in regrowth stands. In contrast, several previous studies have suggested that bats avoid young regrowth plantations due to the high levels of vegetation clutter which restricts their movement and interfere with echolocation (Law and Chidel, 2006; Law et al., 2011; Webala et al., 2011). This makes such areas particularly unsuitable for gleaning and hawking species (Adams et al., 2009; Rainho et al., 2010; Webala et al., 2011). *Pipistrellus* spp., which accounted for over 80% of recorded bat activity in our study, are hawking bats and usually avoid cluttered habitats (Abbott et al., 2012; Norberg and Rayner, 1987) but are also able to forage in the canopy (Plank et al. 2011; Staton and Poulton 2012). Kalko and Schnitzler, (1993) showed that pipistrelle species can adjust their echolocation according to the cluttered environment, making them a more adaptable group in a complex habitat, with the same described for *P. kuhlii* (Berger-Tal et al., 2008). Cluttered environments are often associated with great abundance and diversity of insects (Grindal, 1996; Müller et al., 2012), and in areas where food resources are generally low, such as the eucalypt plantations in our study area, they may adapt their foraging behaviour to exploit these more cluttered habitats.

Other variables that ranked high in the averaged model of bat activity were slope and time since civil twilight. Steep areas showed lower bat activity, as observed in previous studies for *P. pipistrellus* and *P. pygmaeus* (Sattler et al., 2007). These areas are more exposed to extreme weather conditions such as strong winds when compared to gentler slope areas, and may offer less protection for bats and for their

insect prey, making them less appropriate forage areas due to increased energy costs and more difficult manoeuvrability (Russ et al., 2003). Time since civil twilight had a negative influence on all of the response variables. Many bat species feed primarily on dipteran flies, and dipteran activity peaks at dusk. Bat species that feed primarily on dipterans, such as pipistrelles (Barlow, 1997; Goiti et al., 2003; Lisón and Calvo, 2013), emerge early in the evening to maximise their access to these prey (Bartonicka and Rehak, 2004; Jones and Rydell, 1994; Rydell et al., 1996).

The impact of forest plantations on bats and the development of best-practice management guidelines have been studied extensively in some countries, such as the United States (e.g. Hein et al., 2009) and Australia (e.g. Law et al., 2011; Lindenmayer and Hobbs, 2004). Our results support previous studies that have shown a preference of bats for native forests over eucalypt plantations (Hobbs et al., 2003; Law and Chidel, 2006). Our study showed additionally that in dry areas such as the Mediterranean, the availability of water sources is of critical importance to promote bat activity. Our observations of the positive effect of vegetation clutter on bat activity highlight the potential importance of local context in understanding bat distribution and activity. Importantly, these clear associations between bat activity and certain ecological and structural characteristics of eucalypt stands suggest that bat diversity and activity in exotic plantation forests can be promoted through appropriate management. Specifically, favourable conditions for bats can be provided through (1) provision of a high density of water points; (2) maintenance of plots of mature plantations; and (3) promotion of understorey clutter. In order to reach the mean values of bat and *P. kuhlii* activity in mature stands, 0.96 and 0.38, respectively (Table S2), high-level tree clutter must be over 80% and low-level understorey clutter must cover 60% of the stands. In the case of water points, one water point every 500-600 metres increases the bat activity to the levels found in mature stands. To develop integrated forest management strategies incorporating effective bat conservation, we also need to understand how insect prey is distributed along the vertical and horizontal gradients within eucalypt stands and relate it to bat habitat use and diet. Finally, it is important to understand the importance of stand size and connectivity for bat populations, especially in relation to young and mature stands, which are particularly important for bat foraging activity.

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SUPPLEMENTARY MATERIAL

Table S1

Description of the random, explanatory and response variables used to model bat activity, species richness and *Pipistrellus kuhlii* activity.

Explanatory variable name	Variable acronym	Type	Detail description	Transformation
RANDOM VARIABLE				
Midpoints	Midpoints	Nominal	Four midpoints per 1 km transect, ensuring 1 midpoint per 250 metres, totalling 52 midpoints. A buffer of 30 metres radius around each 1 km transect divided it in 4 equal plots and determined the midpoint. A total of 20 random points equally distributed amongst these four plots were evaluated for the studied variables	
Stand variable				
Tree height	TH	Continuous	Tree height, in metres, was determined by measuring the nearest tree to the random point with a laser range finder (Nikon forestry 550, Nikon, Tokyo, Japan)	
Canopy	CAN	Proportion	Measured visually on a scale from 0 to 100%	
Diameter at breast height	DBH	Continuous	Using measuring tape at 1.3m over bark, measured in cm	
Shrub cover	SC	Proportion	Shrub cover was estimated with a square defining 1 square of 1 m^2	Angular
Herb cover	HC	Proportion	Herb cover was estimated with a square defining 1 square of 1 m^2	

Table S1

Cont.

Explanatory variable name	Variable acronym	Type	Detail description	Transformation
Low-level understorey clutter (0-1m)	ClutterLow	Proportion	A 3-m pole with twelve 0.25-m subsections was marked to indicate different heights (Lloyd et al., 2006). If foliage or stems of the understorey touched a subsection, then the subsection was counted and then averaged for each height category	
High-level understorey clutter (1-3m)	ClutterHigh	Proportion	As explained above	Angular
Low-level tree clutter (0-1m)	TreeClutterLow	Proportion	A 3-m pole with twelve 0.25-m subsections was marked to indicate different heights (Lloyd et al., 2006). If foliage or stems of the tree touched a subsection, then the subsection was counted and then averaged for each height category	
High-level tree clutter (1-3m)	TreeClutterHigh	Proportion	As explained above	
Very high-level tree clutter (>3m)	TreeClutterVeryHigh	Proportion	As explained above	

Table S1

Cont.

Explanatory variable name	Variable acronym	Type	Detail description	Transformation
Landscape variables				
Nearest water point	NW	Continuous	The distance to the nearest water point was determined from each midpoint to the nearest permanent water point using the Geographic Information System software ARCMAP 10 (Esri, Redlands, CA, USA), either a pond or a river, in metres. The presence of water points was assessed on Google Earth and validated on the field	
Aspect	ASPECT		Obtained from GIS data of the study area, in degrees	
Slope	SLOPE		Obtained from GIS data of the study area, in degrees	
Survey variables				
Temperature	T	Continuous	Temperature in ºC taken in the beginning of each survey	
Civil twilight	CT	Continuous	Time in minutes that the transect started after civil twilight	Logarithmic
RESPONSE VARIABLES				
Bat activity	BA	Continuous	Number of "bat passes" recorded with 10x time expansion ultrasonic bat detector	
Species richness	SR	Continuous	Number of species or complex of species detected in each plot	

Table S1

Cont.

Explanatory variable name	Variable acronym	Type	Detail description	Transformation
Pipistrellus kuhlii activity	PK	Continuous	Number of *Pipistrellus kuhlii* passes	

Table S2

Mean and standard deviation of each of the explanatory variables and response variables per each land cover (mature and young eucalypt stands and clear-cut areas) and the respectively Kruskal-Wallis P-value. Significant difference obtained by the post hoc test between pairs of eucalypt age stands are depicted using the superscripts a, b and c; where columns have the same letter indicates no significant difference

Explanatory variable	Mean ± SD			Kruskal-Wallis P-Value
	Mature	Young	Clear cut	
HABITAT STRUCTURE VARIABLES				
Tree height (m)	11.17±2.66[a]	5.48±1.18[b]	3.41±1.06[c]	<0.001
Diameter at breast height (cm)	39.35±10.53[a]	23.57±5.30[b]	11.67±4.92[c]	<0.001
Canopy	0.36±0.11[a]	0.12±0.11[b]	0.07±0.08[b]	<0.001
Shrub cover	0.18±0.13[a]	0.26±0.23[a]	0.09±0.10[b]	<0.001
Herb cover	0.07±0.07[a]	0.09±0.11[a]	0.14±0.14[b]	<0.001
Low-level understorey clutter	0.31±0.24[a]	0.34±0.33[a]	0.32±0.23[a]	0.71
High-level understorey clutter	0.15±0.12[a]	0.10±0.15[b]	0.02±0.03[c]	<0.001
Low-level tree clutter	0.31±0.24 [a]	0.34±0.33 [a]	0.25±0.14 [a]	0.75
High-level tree clutter	0.13±0.16[a]	0.79±0.18[b]	0.78±0.32[b]	<0.001
Very high-level understorey clutter	0.27±0.07[a]	0.16±0.06[b]	0.06±0.05[c]	<0.001
Nearest water point (m)	540.25±281.27[a]	931.39±520.14[b]	612.65±364.32[a]	<0.001
Aspect (degrees)	173.60±72.31[a]	104.70±86.00[b]	159.47±112.55[a]	<0.001
Slope (degrees)	6.24±3.78[a]	3.22±2.45[b]	9.86±4.97[c]	<0.001
SAMPLING VARIABLES				
Temperature (ºC)	22.94±5.82 [a]	21.44±5.59 [a]	21.41±4.94 [a]	0.08
Civil twilight (minutes)	51.36±39.04[a]	31.03±30.66[b]	32.79±27.35[b]	<0.001
RESPONSE VARIABLES				
Bat activity	0.96±2.20 [a]	0.64±1.17 [a]	0.28±0.64 [a]	0.004
Species richness	0.56±0.93 [a]	0.40±0.68 [a]	0.22±0.48 [a]	0.005
Pipistrellus kuhlii activity	0.38±1.08 [a]	0.33±0.79 [a]	0.17±0.46 [a]	0.40

Table S3

Summary of models showing Akaike information criteria corrected for small samples (AIC_c). For each response variable (bat activity, species richness, *Pipistrellus kuhlii* activity) is presented the model description, the number of estimable parameters (K), the sample-size adjusted AIC (AIC_c), Akaike differences (ΔAIC_c), Akaike weights and the log-likelihood. Only models with weight above 90% are displayed here

Model	K	AIC_c	ΔAIC_c	Akaike weight	Log-likelihood
Bat Activity					
TreeClutterHigh+ClutterLow+CT+NW+SLOPE+T+TH+random variable	10	691.7	0	0.43	-335.51
TreeClutterHigh+ClutterLow+CT+NW+SLOPE+T+TH+SC+random variable	11	692.8	1.15	0.24	-335.01
TreeClutterHigh+ CT+ NW+SLOPE+ T+ TH+ TreeClutterLow+ random variable	10	693.9	2.22	0.14	-336.62
TreeClutterHigh+ ClutterLow+ CT+ NW+SLOPE+ TH+ random variable	9	696.4	4.70	0.04	-338.92
TreeClutterHigh+ ClutterLow+ CT+ NW+SLOPE+ T+ SC+DBH+ random variable	11	697.0	5.29	0.03	-337.09
TreeClutterHigh+ ClutterLow+ CT+ NW+SLOPE+ TH+ SC+ random variable	10	697.5	5.78	0.02	-338.40
Species richness					
TreeClutterHigh+ClutterLow+NW+SLOPE+T+TH+random variable	9	525.7	0	0.10	-253.60
TreeClutterHigh+ClutterLow+NW+T+TH+random variable	8	525.7	0.01	0.10	-254.66
TreeClutterHigh+ClutterLow+NW+SLOPE+T+TH+CT+random variable	10	526.2	0.49	0.08	-252.78
TreeClutterHigh+ClutterLow+NW+T+TH+CT+random variable	9	526.3	0.55	0.08	-253.87
TreeClutterHigh+NW+T+TH+TreeClutterLow+random variable	8	526.5	0.74	0.07	-255.03
TreeClutterHigh+NW+SLOPE+T+TH+TreeClutterLow+random variable	9	526.8	1.06	0.06	-254.13
TreeClutterHigh+NW+T+TH+CT+TreeClutterLow+ random variable	9	526.9	1.21	0.06	-254.20
TreeClutterHigh+NW+SLOPE+T+TH+CT+TreeClutterLow+random variable	10	527.2	1.48	0.05	-253.28
TreeClutterHigh+ClutterLow+NW+T+TH+ClutterHigh+random variable	9	527.4	1.64	0.05	-254.42
TreeClutterHigh+ClutterLow+NW+T+TH+ASPECT+random variable	9	527.6	1.87	0.04	-254.54

TreeClutterHigh+NW+T+TH+TreeClutterLow+ClutterHigh+random variable	9	527.7	1.96	0.04	-254.58
TreeClutterHigh+NW+T+TH+ClutterLow+HC+TH+ random variable	9	527.7	2.01	0.04	-254.60
TreeClutterHigh+NW+T+TH+SC+ ClutterLow+ TH+ random variable	9	527.8	2.02	0.04	-254.61
TreeClutterHigh+NW+T+TH+TreeClutterLow+HC+TH+ random variable	9	528.3	2.56	0.03	-254.88
TreeClutterHigh+NW+T+TH+ ClutterLow+DBH+ random variable	8	529.2	3.44	0.02	-256.38
TreeClutterHigh+NW+T+TH+ClutterHigh+ DBH+ random variable	8	529.3	3.61	0.02	-256.46
TreeClutterHigh+NW+T+TH+CT+ ClutterLow+ DBH+ random variable	9	529.8	4.01	0.01	-255.61
TreeClutterHigh+NW+T+TH+ClutterHigh+ ClutterLow+ DBH+ random variable	9	529.9	4.17	0.013	-255.69
TreeClutterHigh+NW+T+TH+ ClutterLow+ DBH+SLOPE+random variable	9	530.2	4.41	0.011	-255.81
Pipistrellus kuhlii activity					
ASPECT+TreeClutterHigh+ClutterLow+NW+SLOPE+T+TH+random variable	10	418.00	0.00	0.06	-198.65
ASPECT+TreeClutterHigh+ClutterLow+NW+SLOPE+T+TH+HC+random variable	11	418.50	0.53	0.04	-197.84
TreeClutterHigh+ClutterLow+NW+SLOPE+T+TH+random variable	9	418.50	0.54	0.04	-199.98
TreeClutterHigh+ClutterLow+NW+T+HC+DBH+random variable	9	418.90	0.90	0.04	-200.16
TreeClutterHigh+ClutterLow+NW+SLOPE+T+TH+HC+random variable	10	418.90	0.98	0.04	-199.14
ASPECT+TreeClutterHigh+NW+SLOPE+T+TH+random variable	9	419.30	1.34	0.03	-200.38
TreeClutterHigh+ClutterLow+NW+T+TH+random variable	8	419.40	1.43	0.03	-201.48
ASPECT+TreeClutterHigh+NW+SLOPE+T+TH+TreeClutterLow+random variable	10	419.50	1.50	0.03	-199.40
TreeClutterHigh+NW+T+HC+ClutterHigh+random variable	8	419.50	1.52	0.03	-201.52
ASPECT+TreeClutterHigh+ClutterLow+NW+SLOPE+T+TH+CT+random variable	11	419.50	1.55	0.03	-198.36
TreeClutterHigh+ClutterLow+NW+T+TH+HC+CT+random variable	10	419.50	1.56	0.03	-199.43
TreeClutterHigh+ClutterLow+NW+T+HC+DBH+CT+random variable	10	419.60	1.64	0.03	-199.47
ASPECT+TreeClutterHigh+ClutterLow+NW+SLOPE+T+HC+DBH+random variable	11	419.70	1.71	0.02	-198.43

ASPECT+TreeClutterHigh+ClutterLow+NW+SLOPE+T+TH+HC+CT+random variable	12	419.90	1.90	0.02	-197.46
TreeClutterHigh+ClutterLow+NW+SLOPE+T+TH+HC+CT+random variable	11	419.90	1.95	0.02	-198.56
NW+T+ TreeClutterHigh+ ClutterHigh+ASPECT+SLOPE+TH+ random variable	10	420.10	2.13	0.02	-199.71
NW+T+ TreeClutterHigh+ ClutterHigh+ HC+ ASPECT+ SLOPE+ random variable	10	420.20	2.20	0.02	-199.75
NW+T+ TreeClutterHigh+ SC+ ClutterLow+DBH+ HC+ random variable	10	420.30	2.35	0.02	-199.82
NW+T+ TreeClutterHigh+ HC+ ASPECT+ SLOPE+ TH+ random variable	10	420.40	2.40	0.02	-199.85
NW+T+ TreeClutterHigh+ ClutterHigh+ HC+CT+ random variable	9	420.40	2.43	0.02	-200.92
NW+T+ TreeClutterHigh+ SC+ ClutterLow+ HC+ ASPECT+ SLOPE+ TH+ random variable	12	420.40	2.45	0.02	-197.73
NW+T+ TreeClutterHigh+ ClutterLow+ DBH+ HC+ ASPECT+ random variable	10	420.40	2.47	0.02	-199.88
NW+T+ TreeClutterHigh+ ClutterHigh+ ClutterLow+ DBH+ HC+ random variable	10	420.50	2.52	0.02	-199.91
NW+T+ TreeClutterHigh+ HC+ ASPECT+ SLOPE+ TH+ TreeClutterLow+ random variable	11	420.50	2.57	0.02	-198.87
NW+T+ TreeClutterHigh+ ClutterHigh+ TH+ random variable	8	420.50	2.59	0.02	-202.06
NW+T+ TreeClutterHigh+ ClutterHigh+ ClutterLow+ HC+ TH+ random variable	10	420.60	2.65	0.02	-199.97
NW+T+ TreeClutterHigh+ ClutterHigh+ HC+ SLOPE+ random variable	9	420.60	2.66	0.02	-201.04
NW+T+ TreeClutterHigh+ ClutterHigh+ HC+ TH+ random variable	9	420.70	2.76	0.01	-201.09
NW+T+ TreeClutterHigh+ SC+ ClutterLow+ HC+ TH+ random variable	10	420.80	2.89	0.01	-200.09
NW+T+ TreeClutterHigh+ ClutterHigh+ ClutterLow + HC+ random variable	9	420.90	2.91	0.01	-201.16
NW+T+ TreeClutterHigh+ ASPECT+CT+ SLOPE+ TH+ random variable	10	420.90	2.91	0.01	-200.10
NW+T+ TreeClutterHigh+ ClutterHigh+ DBH+ HC+ random variable	9	420.90	2.92	0.01	-201.17
NW+T+ TreeClutterHigh+ ClutterLow+ HC+ ASPECT+ TH+ random variable	10	420.90	2.92	0.01	-200.11
NW+T+ TreeClutterHigh+ ClutterHigh+ HC+ ASPECT+ random variable	9	421.00	3.04	0.01	-201.23
NW+T+ TreeClutterHigh+ ClutterHigh+ HC+ CANOPY+ random variable	9	421.00	3.05	0.01	-201.23
NW+T+ TreeClutterHigh+ HC+ ASPECT+ SLOPE+ random variable	9	421.00	3.05	0.01	-201.24
NW+T+ HC+CANOPY+ random variable	7	421.00	3.06	0.01	-203.34

NW+T+ TreeClutterHigh+ TH+ random variable	7	421.00	3.08	0.01	-203.35
NW+T+ TreeClutterHigh+ ClutterHigh+ HC+ ASPECT+ SLOPE+ TH+ random variable	11	421.00	3.08	0.01	-199.12
NW+T+ TreeClutterHigh+ TH+ TreeClutterLow+ random variable	8	421.10	3.17	0.01	-202.35
NW+T+ TreeClutterHigh+ SC+ ClutterLow+ DBH+ HC+CT+ random variable	11	421.20	3.27	0.01	-199.21
NW+T+ TreeClutterHigh+ ClutterLow+ DBH+ HC+ ASPECT+CT+ random variable	11	421.30	3.29	0.01	-199.23
NW+T+ TreeClutterHigh+ HC+ TH+ random variable	8	421.30	3.35	0.01	-202.44
NW+T+ TreeClutterHigh+SC+ ClutterLow+ HC+CT+ TH+ random variable	11	421.40	3.42	0.01	-199.29
NW+T+ TreeClutterHigh+ ClutterLow+ HC+ ASPECT+CT+ TH+ random variable	11	421.40	3.45	0.01	-199.31

CHAPTER 4

INFLUENCE OF EXOTIC FOREST PLANTATIONS ON OCCUPANCY AND CO-OCCURRENCE PATTERNS IN A MEDITERRANEAN CARNIVORE GUILD

Preface

Carnivores have frequently been used as flagship species in conservation due to their charismatic value, such as the tiger (*Panthera tigris*) or the giant panda (*Ailuropoda melanoleuca*) (Caro, 2010), but also because of the role they occupy in the food chain, as predators which can have an important impact on structure and functionality of the ecosystem (Duffy, 2003; Miller et al., 2001). One third of world's Carnivore species are classified as Threatened or Near Threatened (IUCN, 2013) and amongst the main threats identified are habitat loss and fragmentation and prey scarcity. In the Mediterranean region, these threats are translated as a scarcity of the main prey, the wild rabbit (*Oryctolagus cuniculus*), which is a keystone species in the region, and habitat destruction and alteration by replacing *montados* with intensive agriculture and forests planted with exotic species like eucalypt (*Eucalyptus* spp.). Habitat changes and lack of usual prey can lead to modifications in the way in which carnivores interact with each other. Niche partitioning among a community of carnivores is essential for their coexistence (Schoener 1974). The intraguild predation theory predicts that top predators distribute themselves according to food availability and subordinate predators according to food availability and safety from predation (Holt & Polis, 1997). In this chapter, I consider niche partitioning in terms of diel activity patterns (Schuette et al., 2013) and space and habitat use (Sarmento et al., 2011). In Mediterranean ecosystems, interactions among sympatric carnivores have been studied extensively, but the impact of major land use change, such as afforestations, on niche partitioning and intraguild predation is less well understood.

In this Chapter, using the red fox (*Vulpes vulpes*)-badger (*Meles meles*)-stone marten (*Martes* foina) guild as a model, I tested the assumptions of niche partitioning theory in a modified landscape dominated by eucalypt plantations, using camera trapping to monitor occupancy and co-interactions of the different species.

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Influence of exotic forest plantations on occupancy and co-occurrence patterns in a Mediterranean carnivore guild

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Abstract

The Mediterranean basin is a biodiversity hotspot which is being threatened by land abandonment and afforestation, most notably with eucalypt plantations. We assessed the impact of eucalypt plantations on niche partitioning in a carnivore community consisting of red fox (*Vulpes vulpes*), badger (*Meles meles*) and stone marten (*Martes foina*). Based on data from camera trapping, we evaluated the influence of eucalypt plantations on species occupancy and detection in single-species and co-occurrence models and on temporal activity. Eucalypt cover negatively influenced detection probability across all species in both single and co-occurrence models. Stone marten detection decreased with the presence of the other carnivores but red fox detection increased in the presence of badger. Eucalypt plantations had a negative effect on occupancy of red fox, which preferred open farmland and evergreen oak forest. Stone marten preferred large patches of oak forest while badger occupancy was positively influenced by patch richness. Occupancy of any one species was not influenced by the presence of any other species. Despite having an effect on the detection and occupancy of all three carnivores, eucalypt plantations had no effect on the interactions within this carnivore community. The results show the relatively greater importance of habitat preferences compared with interspecific relationships in determining distribution of these carnivores, and highlight the importance of using

models that can correct for differences in detectability for inferring interspecific competition, especially when species occur at low densities.

Keywords

Eucalypt; red fox; stone marten; badger; camera trapping; niche partitioning;

Introduction

The Mediterranean basin is a biodiversity hotspot, characterised by a high number of endemic species and a multifunctional mosaic landscape (Myers et al. 2000; Blondel et al. 2010). One of the driving forces for such exceptional biodiversity is anthropogenic disturbance (e.g. grazing, clearcutting, prescribed fire) (Blondel et al. 2010), the impact of which depends on the magnitude, frequency, size of landscape, extent of the disturbance event, dispersion and the rate of recovery (Moloney and Simon 1996; Farina 1998). Historic use of the land by humans has led to the development of evergreen oak savannas (*montados* in Portugal and *dehesas* in Spain). These habitats have a canopy dominated by cork oak (*Quercus suber*) and/or Holm oak (*Quercus ilex*), managed for the production of cork, timber and acorn, with herbaceous layers of annual crops or pastures. However, over recent decades, labour scarcity (Rudel et al. 2005) and agricultural policy with incentives for farmland conversion have led to a polarisation between land intensification (higher grazing pressure, intensive crop farming systems) and land abandonment (Costa et al. 2011). These land use changes have resulted in modifications of the functional and taxonomic diversity of the ecosystems (Hooper et al. 2012), representing a major threat to this biodiversity hotspot. An increase in plantation forests has been one of the major land use changes, and plantations now cover about 11% of the forested area in the Mediterranean (Blondel et al. 2010). The principal plantation species in the area is eucalypt (*Eucalyptus* spp.), an exotic tree, which now covers 10% of mainland Portugal (ICNF 2013) and is usually associated with poor diversity (Ramírez and Simonetti 2011; Calviño-Cancela et al. 2012).

In this paper, we assess the impact of eucalypt plantations on a guild of carnivores within the Mediterranean basin ecosystem by evaluating species occupancy and spatio-temporal intraguild relationships. Several carnivore species are threatened or

their interactions altered by habitat modification, direct persecution, disease and prey depletion. The presence of a biodiverse carnivore community is often regarded as a sign of a healthy ecosystem (Miller et al. 2001) and carnivores can have an important role as sentinel and flagship species (Sergio et al. 2008). Species interactions and use of resources within the same guild are often analysed using niche partitioning theory (Schoener 1974). Niche partitioning can be expressed in several dimensions including habitat, diet and time (Schoener 1974). If there is a considerable overlap between species in one of the dimensions, differences between species in the other dimensions would be expected. Different morphological traits, such as body size and dentition (Donadio and Buskirk 2006; Davies et al. 2007), partitioning of space (Sarmento et al. 2011), temporal pattern segregation (Schuette et al. 2013) and utilisation of different food resources (Foster et al. 2013) have been observed, allowing potential competitor carnivore species to coexist. Intraguild predation theory proposes that, in the event of competition, the dominant predator is distributed according to food resources, while subordinate predators modify their habitat and activity patterns as a consequence (Palomares and Caro 1999), to avoid aggression, kleptoparasitism or both (Gorman et al. 1998; Palomares and Caro 1999; Krofel and Kos 2010).

In Mediterranean ecosystems, relationships among sympatric carnivores have been studied extensively, but the impact of major land use change, such as plantation forestry, on niche partitioning and intraguild predation is less well understood. Eucalypt plantations represent open habitats, with low understorey complexity (Ramírez and Simonetti 2011). They offer inadequate shelter from extreme weather conditions and other predators (such as dogs or man) (Mangas et al. 2008) and are characterised by low food availability (fruits, insects and small mammals) (Rosalino et al. 2005c; Pereira et al. 2012). These characteristics may affect the behaviour of species in eucalypts, since the habitat demands greater foraging effort and poses a higher predation risk.

Mesopredators can play an important role on the ecosystem, especially when top predators are absent (Pasanen-Mortensen et al. 2013). In our study area, top predators such as the Iberian lynx (*Lynx pardinus*) or wolf (*Canis lupus*) have been extirpated for over a decade now. The carnivore community in the region comprises such

species as the red fox (*Vulpes vulpes*), badger (*Meles meles*) or stone marten (*Martes foina*) amongst others.

The red fox has the largest distribution of all the Carnivore species, covering nearly 70000 km^2, it is an opportunistic forager and an habitat generalist (Macdonald and Sillero-Zubiri 2004). Its home range vary according to the region, season, prey availability and sociality seems to be restricted to co-operation in the raising of cubs (Cavallini 1996). Stone marten and badger's distribution are also widespread occurring throughout much of Europe and central Asia. Stone marten, a small, solitary carnivore, weighting less than 2.5 kg, has an average home range that varies between 210-230 ha, preferring open deciduous forests and rock outcroppings (Libois and Waechter 1991). These mustelids are opportunistic, omnivorous species, and their diet varies with season and availability. Badger prefers open habitats and deciduous woodlands, with an average home range of 446 ha, living in social groups of 3-4 adults plus cubs (Rosalino et al. 2004).

Using the red fox-badger-stone marten guild as a model, we tested the assumptions of niche partitioning theory in a modified landscape dominated by eucalypt plantations, using camera trapping to monitor occupancy of the different species. Predation by red fox on marten (*Martes martes*), a carnivore similar to stone marten, (Lindström et al. 1995) and aggressive behaviour of badger towards red fox (Macdonald et al. 2004) have been described in Northern European ecosystems. Based on these previously recorded relationships, we predicted that:

1. Badger occupancy, detection and behaviour would not be influenced by the presence of the other two predators, but solely by land cover and landscape structure, with badgers preferring heterogeneous habitat and avoiding eucalypt plantations (Fig. 1);
2. The red fox would show avoidance of eucalypt plantations relative to other habitats, but would also adjust its activity patterns and habitat occupancy to avoid badgers (Fig. 1);
3. Stone marten would show a preference for native forested and homogeneous habitat, avoiding eucalypt plantations due to its greater vulnerability to

predation in this habitat, and would show avoidance of both red fox and badger (Fig. 1);

4. The probability of detection for each carnivore would be lower in eucalypt plantations than in the remaining native habitats (Fig. 1).

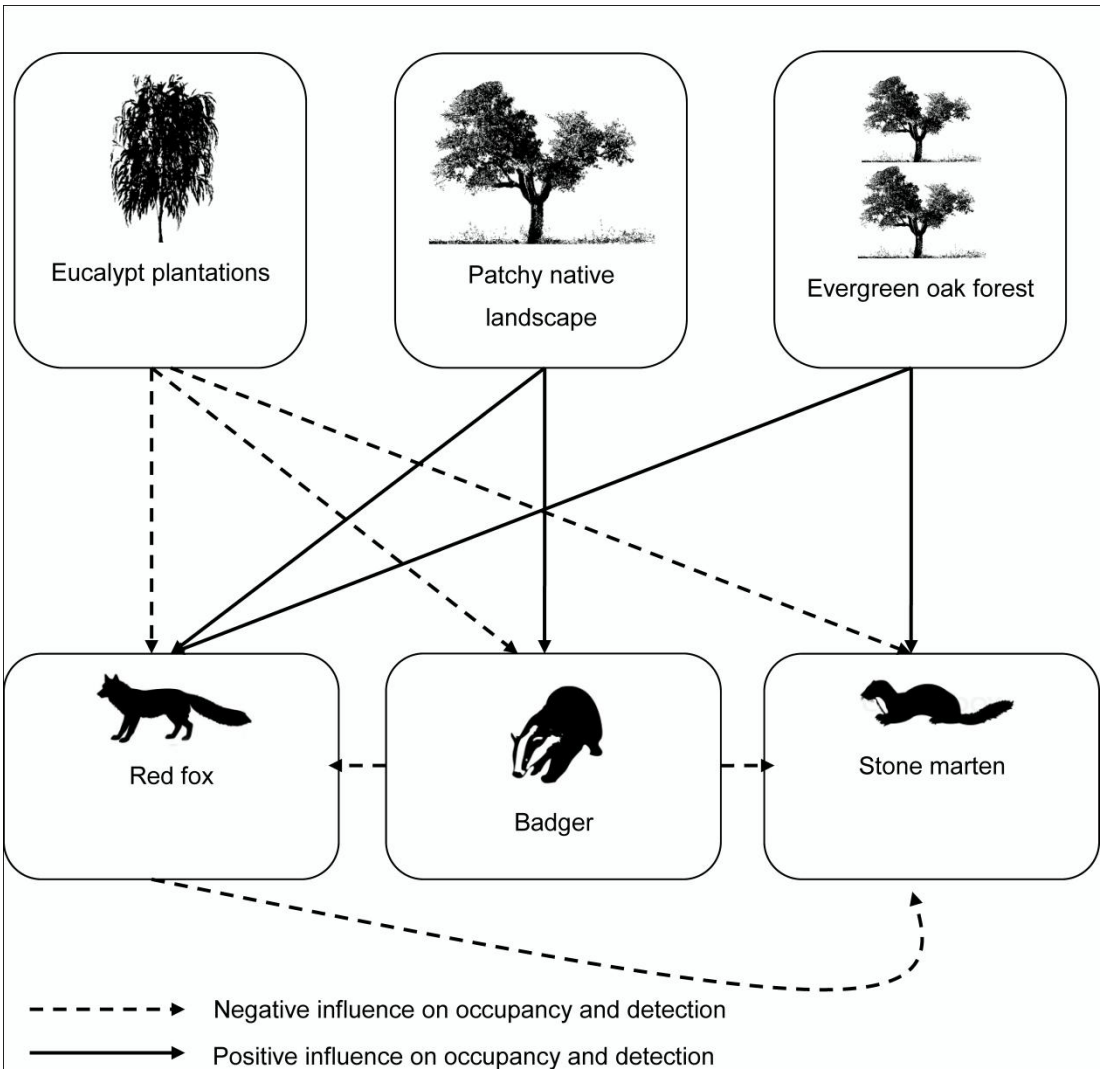

Fig. 1 Diagram with the hypotheses tested. Eucalypt plantations are expected to negatively influence occupancy and detection probability of red fox, *Vulpes vulpes*, badger, *Meles meles* and stone marten, *Martes foina*. Badger would prefer patchy landscapes while stone marten would occupy large patches of wooded area. Badger would negatively influence both occupancy and detection of red fox and stone marten, and red fox would have the same effect on stone marten

To assess these predictions we used multi-season single-species occupancy modelling (MacKenzie et al. 2002) to analyse which factors influenced occupancy while accounting for imperfect detectability. We then modelled co-occurrence to evaluate species interactions (Richmond et al. 2010). Finally, we determined the activity patterns of the three carnivores to evaluate the existence of temporal segregation (Linkie and Ridout 2011).

Materials and methods

Site description

We conducted the study in two sites (Sites A and B) in central-east Portugal, Castelo Branco district (39º38'–39º42'N, 7º10'–7º22'W) (Fig. 2), which is characterised by a Mediterranean climate.

The land cover is dominated by eucalypt plantations, with different age stands, cork oak and Holm oak forest and *montados* (oak savannah-like woodland). In smaller, dispersed patches there are also olive (*Olea europaea*) yards, scrubland areas dominated by *Cytisus* spp., *Cistus* spp. and *Erica* spp. and open farmlands mainly cultivated with wheat (*Triticum* spp.). The area is managed for big game, essentially red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*), with the animals being fed artificially. Site A is dominated by eucalypt and it is fenced, but still porous to these species, while the land cover on Site B is mainly evergreen oak forests and *montados* (Fig. 2).

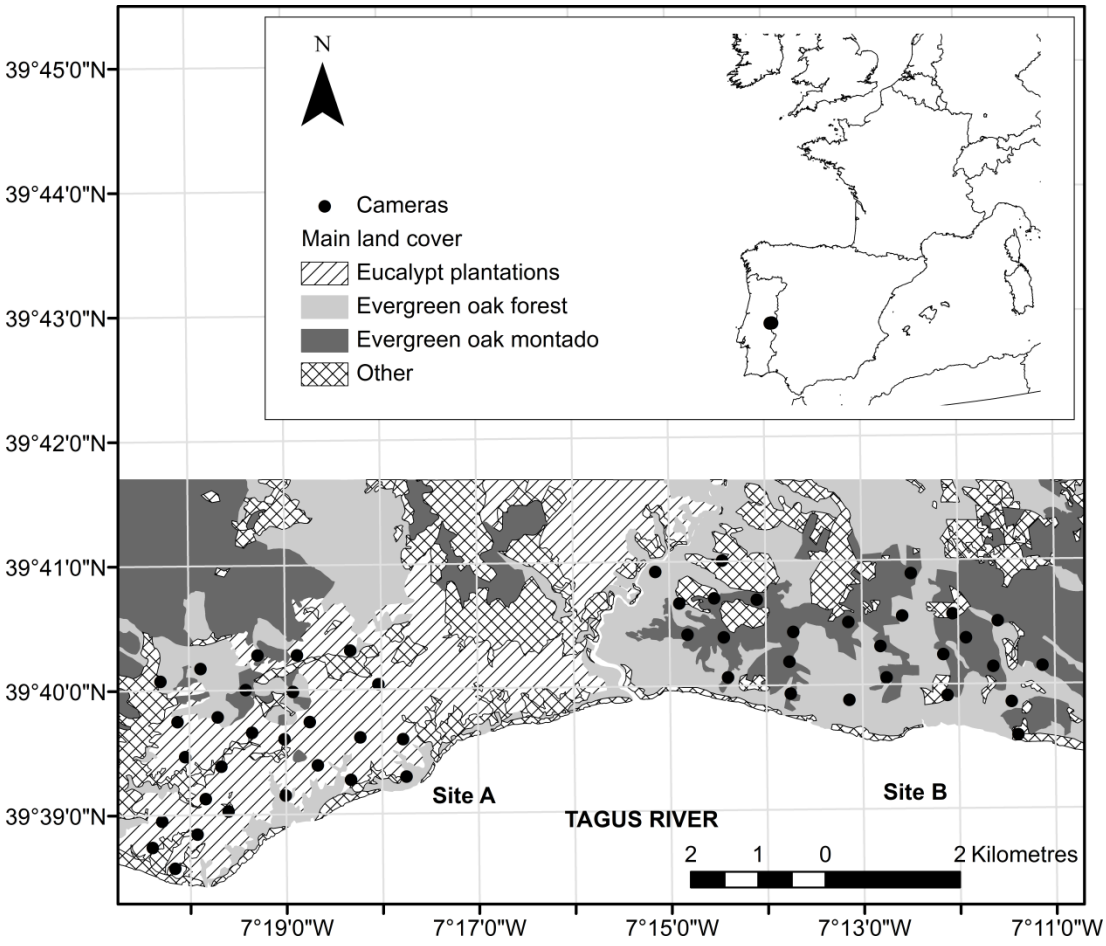

Fig. 2 Study area and the location of the camera traps in central-east Portugal, 2011/2012. Site A is dominated by eucalypt plantations and Site B by evergreen oak forests and montados. Inset shows general location of the study area in Portugal

Camera trapping

Carnivore presence was assessed between March and July 2011, and May and June 2012, using baited camera traps (Bushnell Trophy Cam, Bushnell Corporation, Overland Park, Kansas, USA) (Table 1).

The use of bait or olfactory lures to attract animals is commonly used in camera-trapping studies since it increases detectability and consequently survey efficiency for some species such as red fox (Bischof et al. 2014b), but it is also used for others species such as stone marten (Santos and Santos-Reis 2010; Sarmento et al. 2011; Bischof et al. 2014a) and badger (Monterroso et al. 2013). Species may, however, respond differently to the same bait as demonstrated by Monterroso et al. (2011).

Table 1 Data for the four camera trap surveys carried out in central-east Portugal

Sites	Trapping Period	Camera days	Number of cameras	Mean inter-camera distance (m)
A	20/03/2011 – 26/04/2011	962	26	567
	06/05/2012 – 05/06/2012	780	26	567
B	12/06/2011 – 11/07/2011	754	26	657
	05/06/2012 – 30/06/2012	442	17	540

The mean inter-camera distance was chosen to adequately sample the target species, considering a buffer area of half the species home-range diameters to represent the total surveyed area by that set of camera traps (Karanth and Nichols 1998). Buffer area diameters were obtained from previous studies in our area and from studies performed in similar environments and available in the literature: 600 m for red foxes (Sarmento et al. 2011), 550 m for stone martens (Santos-Reis et al. 2005) and 600 m for badgers (Rosalino et al. 2004).

The cameras were placed in trees, at 30 cm above ground, along dirt roads, trails, ponds and streams to maximize photo captures, with dry cat and dog food as bait. The cameras were checked weekly to replace batteries and renew the bait. Each camera was set to record a video for 10s, with a time delay of 30s between each video. The date and time of each video were also recorded. Recorded videos were scanned and the camera station, date, time, species and number of any animals recorded were entered into Camera Base version 1.5 (Tobler 2012) for data management and analysis. Photos of the same species taken by the same camera more than 60 minutes apart were treated as independent for the analysis (Towerton et al. 2011).

Explanatory variables

We divided the explanatory variables into two groups: (1) landscape cover; and (2) landscape structure within a 1000m buffer around the camera locations (see Supplementary Material Table S1). Landscape structure was measured in terms of area, edge length, aggregation and diversity, using FRAGSTATS software at an 8-m cell resolution (McGarigal et al. 2012).

Single-species occupancy models

We estimated fox, badger and stone marten occupancy (ψ) using a likelihood-based two-season occupancy model (MacKenzie et al. 2003). Dynamic occupancy models estimate four parameters: occupancy (ψ), colonisation (δ), extinction (ε) and detection probability (ρ) using a likelihood-based method adapted to imperfect detectability (MacKenzie and Royle 2005). In each site (cameras) species detections were coded as 1 (detection of target species) and 0 (non-detection of target species). Then the records were transformed into detection histories for each site ($\mathbf{X}_i$) which were used with a product multinomial likelihood model, to estimate occupancy parameters, as follows:

$$\mathbf{L}(\psi_1, \varepsilon, \delta, \rho \mid X_1, \ldots Xn) = \pi_{i=1} \mathbf{Pr}(X_i)$$

where ψ_1 is a vector of site occupancy probabilities for the first primary sampling period, ε and δ are matrices of local extinction and colonisation, and ρ is a matrix of detection probabilities.

Considering that we only had data for two seasons and that we observed a considerable stability in occupancy for the three species we just modelled the seasonal occupancy and detection parameters.

We ran analyses in program MARK (White and Burnham 1999) using multiple-season models, including covariate effects. The study was divided into primary and secondary occasions. For each season we considered six primary occasions (we assumed that occupancy does not change between them) that each consisted of 7 days' continuous sampling. The secondary occasions corresponded to each sampling season (2011 and 2012). The data were analysed using a 2-step approach (Sarmento et al. 2011). Firstly, we calculated the outcome of season and landscape cover covariates on detection probabilities, while keeping occupancy constant (i.e. ψ [.]ρ [*variable*]). Considering that land cover can influence movement patterns (Sollmann et al. 2012), we tested all possible effects of these covariates in detection. Secondly, we used the best-fitting model for detection probabilities and combined it with a set of a priori models integrating covariates to explain the observed patterns of occupancy.

All continuous covariates were standardized to z-scores prior to analysis. To assess collinearity, we used the Spearman rank correlation coefficient since it makes no assumption about linearity between two variables (Zuur et al. 2009); we used a value of ±0.6 to indicate high collinearity and excluded highly correlated variables from the same models.

The ranking of candidate models was performed using the Akaike Information Criterion corrected for small sample size (AIC_c) by calculating their Akaike's weights (ω) (Burnham et al. 2011). Models with Δ AIC_c values ≤ 2 compared with the most parsimonious model were classified as robustly supported. Akaike´s weights were used to further interpret the relative importance of each model´s independent variable. Likelihood ratio tests were used to compare models representing the tested hypotheses by comparing the difference in deviance (-2logL) between pairs of models to the critical value of the χ^2 distribution. The selected models allowed the calculation of the average estimates of seasonal occupancy and detection probabilities. Only those explanatory variables, for which 95% confidence intervals around the estimate of beta did not overlap zero, were considered in the ranking of the occupancy models. We tested the effect of each covariate in occupancy separately and then, according to the results of AIC_c estimates and the significance of the beta coefficients, we constructed several models with an additive combination of covariates, testing a total of 45 models for each species.

Two-species occupancy models

Following the previous analysis, we investigated potential species interactions using two-species occupancy conditional models implemented in MARK. Our objectives were to test hypotheses about competition and to quantify patterns of interaction by estimating a series of co-occurrence parameters (Richmond et al. 2010):

1. ψ^A - Probability of occupancy for species A (the potential dominant species);
2. ψ^{BA} - Probability of occupancy for species B, given species A is present;
3. ψ^{Ba} - Probability of occupancy for species B, given species A is absent;
4. p^A - Probability of detection for species A, given species B is absent;
5. p^B - Probability of detection for species B, given species A is absent;
6. r^A - Probability of detection for species A, given both species are present;

7. r^{BA} - Probability of detection for species B, given both species are present and species A is detected;
8. r^{Ba} - Probability of detection for species B, given both species are present and species A is not detected.

These models permit the calculation of a species interaction factor (SIF – φ), according to the equation:

$$\varphi = (\psi^{A}\,\psi^{BA})/(\psi^{A}\,\psi^{BA} + (1-\psi^{A})\,\psi^{Ba})$$

This parameter represents the ratio of the probability of the species A and B co-occurrence in a site compared to the one expected if they occur independently. When $\varphi < 1$, the species co-occur less frequently than expected. Considering co-occurrence, we hypothesised that stone martens (ST) could avoid areas intensively used by foxes (RF) and badgers (B) and foxes could avoid badgers (Macdonald et al. 2004). This can be translated as: (1) the subordinate species appears less frequently ($\varphi < 1$ and $\psi^{STRF} < \psi^{STrf}$ and/or $\psi^{STB} < \psi^{STb}$ and/or $\psi^{RFB} < \psi^{RFb}$) than if it occupied sites independently or (2) its detection is lower in areas where the dominant species is present ($r^{STRF} < r^{STrf} < p^{ST}$ or $r^{STB} < r^{STb} < p^{ST}$ or $r^{RFB} < r^{RFb} < p^{RF}$). Detection was also modelled as a function of eucalypt cover. Model selection and analysis were conducted using the approach described above.

Temporal co-occurrence

To estimate the daily activity overlap patterns of the three carnivores, we used the two-step methodology developed by Ridout and Linkie (2009). Firstly, each activity pattern was estimated using kernel density estimates, applying the smoothing parameter of 1.00. Secondly, we calculated the coefficient of overlap (Δ), varying between 0 (if one species is diurnal and the other nocturnal, for example) and 1 (identical patterns) for a full day (24 hours) and for the activity period only, between 18:00 and 6:00. Of the several estimators presented by Ridout and Linkie (2009), we used the one best suited for small sample size (Δ_1) which is defined as:

$\Delta_1 = \int_0^1 min\{\hat{f}\,(t), \hat{g}\,(t)\}\,dt$, where $\hat{f}\,(t)$ and $\hat{g}\,(t)$ are the two activity functions of time *t* being tested.

The scripts to run the daily activity patterns were adapted from Linkie and Ridout (2011), available from http://www.kent.ac.uk/smsas/personal/msr/overlap.html.

All statistical analyses were run using the software R 2.15 (R Development Core Team 2012), unless stated otherwise.

Results

With an effort of 2938 trap nights, we recorded 652 independent detections of five carnivores: red fox (527), badger (54), stone marten (49), Egyptian mongoose (*Herpestes ichneumon*) (15) and genet (*Genetta genetta*) (7).

Single-species occupancy models

Mean detection probability was different amongst red fox, stone marten and badger (Fig. 3). Red fox had the highest detection probability (mean±SE: 0.60±0.02), stone marten showed significant differences according to each season sampled (2011: 0.09±0.02; 2012: 0.31±0.05), and badger had one of the lowest detection probabilities (0.13±0.03).

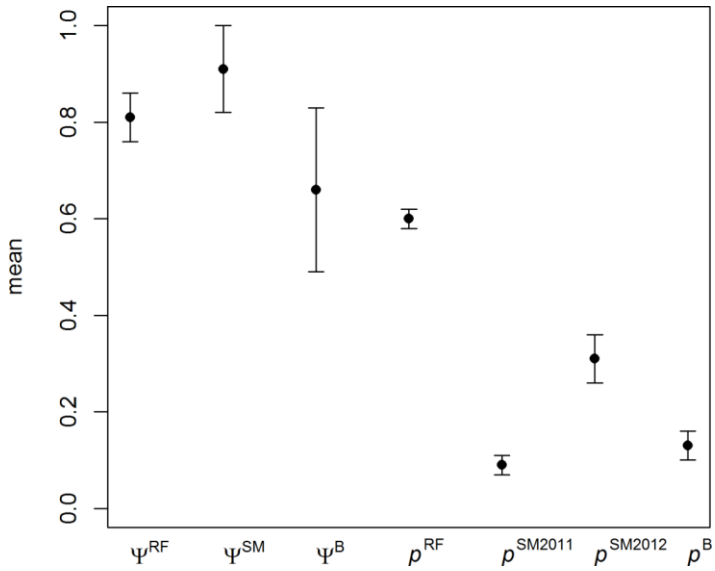

Fig. 3 Mean and standard error (±) for the probability of occupancy (ψ), and detection (p) of red fox (RF), stone marten (SM) for 2011 and 2012, and badger (B)

Apart from season, which only influenced stone marten detection, the percentage of eucalypt cover was the only covariate that influenced negatively the detection probability for all three species (Fig. 4).

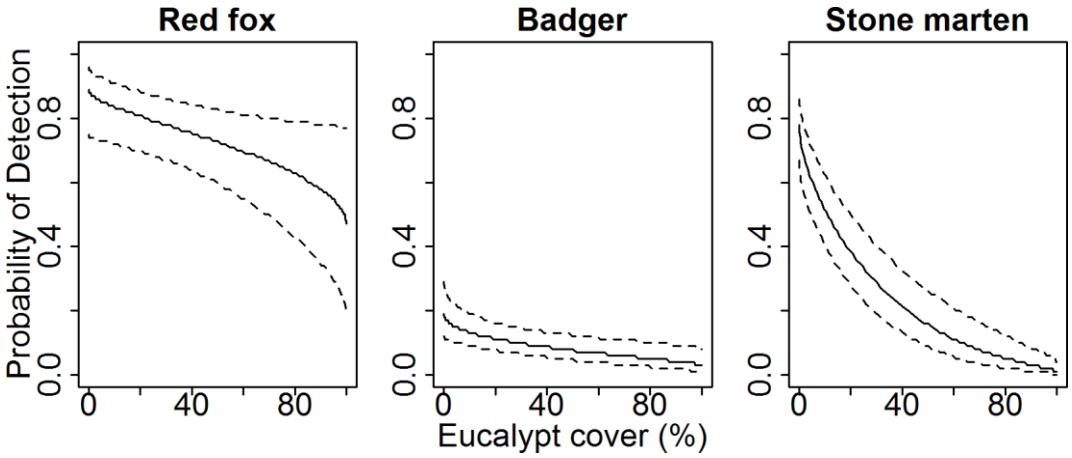

Fig. 4 Estimated probability of detection as a function of eucalypt cover (%) for each carnivore studied (red fox, badger and stone marten). This figure shows how the increase of eucalypt cover decreases detectability for all three species

Occupancy was mainly explained by land cover for red fox and stone marten (Table 2; Fig. 5). Red fox occurrence was negatively correlated with eucalypt cover and positively correlated with open farmland and oak forest (Fig. 5). Unlike red fox, badger occurrence was not influenced by land cover but mostly influenced positively by patch richness (Table 2; Fig. 5). Stone marten occupancy was positively correlated with the oak forest cover and large patches (Largest Patch Index) (Table 2; Fig. 5), showing a clear preference for large, homogeneous patches of oak forest.

Table 2 Comparison of models exploring the land cover and landscape metrics on occupancy of red fox, badger and stone marten. Only models with $\Delta AIC_c \leq 2$ are shown. -

Model	AIC_c	ΔAIC_c	AIC_c wt	-2logL	K
Red fox					
Ψ(EUC), *p*(EUC)	661.32	0.00	0.21	1.00	5.00
Ψ(OpenFarm), *p*(EUC)	661.45	0.13	0.19	0.94	5.00
Ψ(EUC, OpenFarm),*p*(EUC)	661.54	0.22	0.18	0.90	6.00
Ψ(OakFor), *p*(EUC)	661.72	0.40	0.17	0.82	5.00
Ψ(EUC, OakFor), *p*(EUC)	663.33	2.00	0.08	0.37	6.00
Badger					
Ψ(PR), p(EUC)	284.61	0.00	0.32	1.00	4.00
Ψ(SHEI), p(EUC)	286.44	1.83	0.13	0.40	4.00
Stone marten					
Ψ(LPI), *p*(Season*Euc)	308.87	0.00	0.31	1.00	7.00
Ψ(LPI, OakFor), *p*(Season*Euc)	310.16	1.30	0.16	0.52	8.00

2log L: 2log-likelihood; K: number of parameters; AIC_c: Akaike's Information Criterion; ΔAIC_c: delta AIC_c; AIC_c wt: AIC_c weight

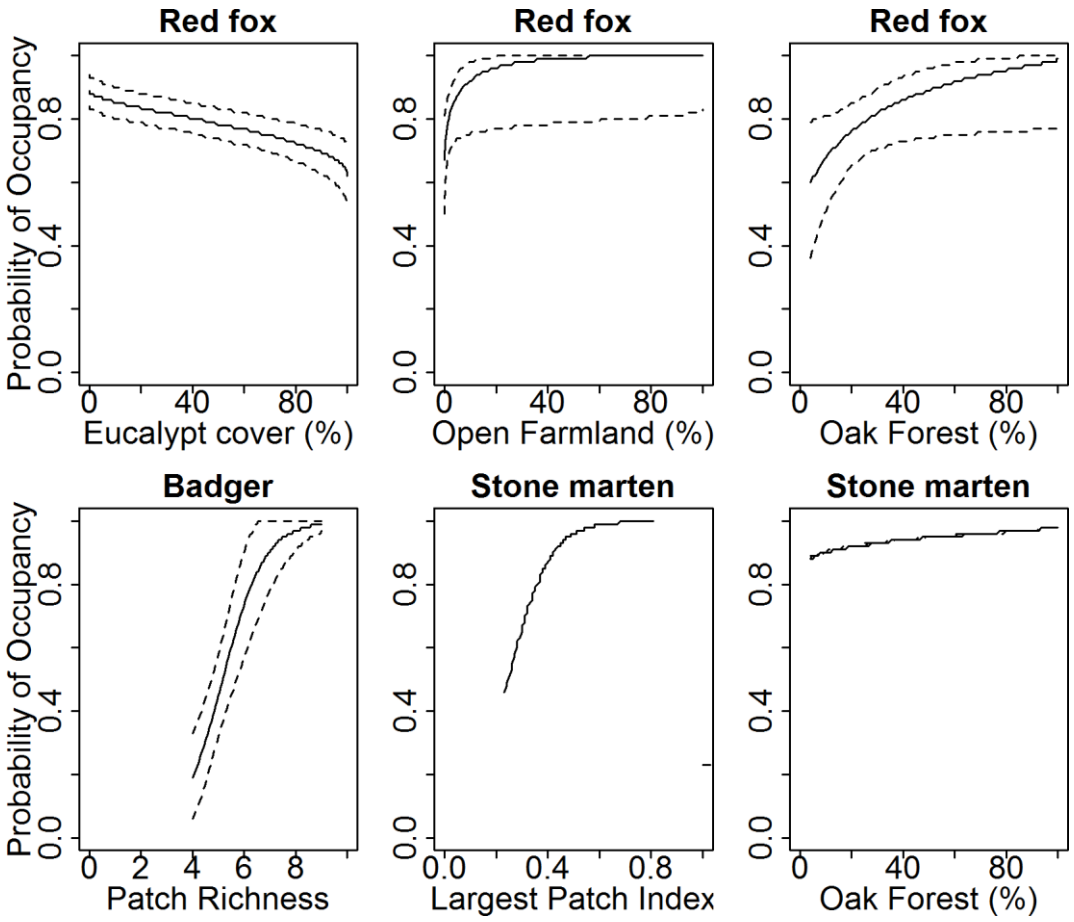

Fig. 5 Estimated probability of site occupancy as a function of eucalypt (%), open farmland (%), and oak forest (%) cover for red fox; patch richness for badger, and largest patch index and oak forest (%) cover for stone marten. Only covariates from the top models ($\Delta AIC_c \leq 2$) and significant were plotted

Species co-occurrence

The presence of red fox had no influence on the occupancy probability for stone marten ($\psi^{STRF} = \psi^{STrf} = 0.52 \pm 0.08$) (Table 3). According to the two best explanatory co-occurrence models, we obtained an φ of 1.00 ± 0.00 suggesting the inexistence of spatial avoidance. The same was not true for detectability. The presence and detection of red fox significantly decreased the detectability of stone marten ($r^{STRF} = 0.06 \pm 0.02$) and this effect was also seen in areas covered by eucalypt ($r^{STRF(Euc)} = 0.05 \pm 0.02$) (Table 3; Fig. 6). In sites where red fox was estimated to be absent or not

detected, the probability of detection of stone marten increased (p^{SM} = r^{SMrf} = 0.23±0.04).

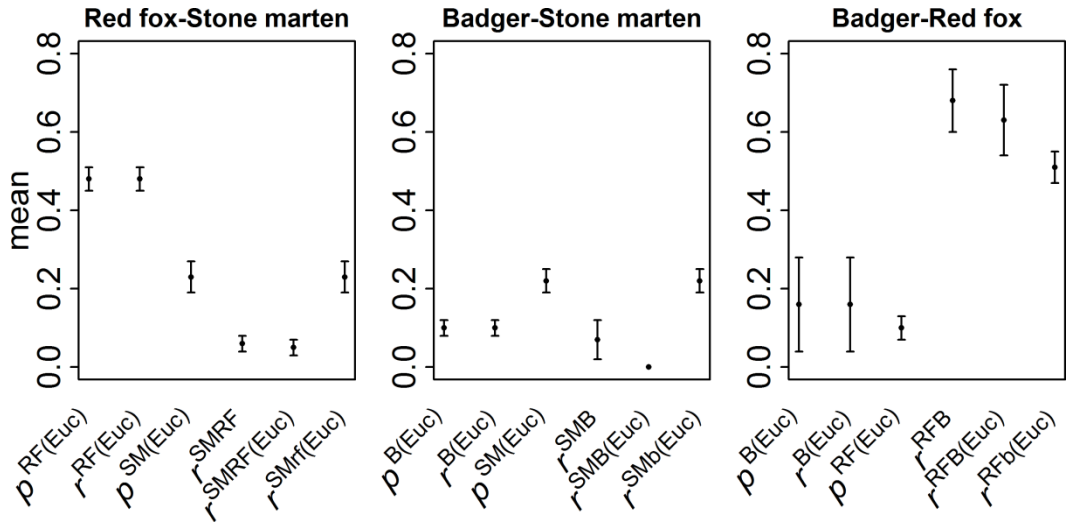

Fig. 6 Probabilities of detection (±SE) estimated from two-species co-occurrence models for red fox-stone marten, badger-stone marten, badger-red fox based on camera-trapping, p = probability of detecting a species given absence of the other species from the site. r = probability of detecting a species given both species are present (capital letter) and/or present but undetected (lower case letter), r was also estimated as a function of eucalypt. RF – red fox; SM – stone marten; B – badger; Euc – eucalypt plantations

For stone marten and badger a similar pattern was observed, with lack of badger influence on stone marten occupancy (ψ^{SMB}= ψ^{SMb} = 0.91±0.08) (Table 3; Fig. 6). The top ranked explanatory model presented an φ of 1.00±0.00 confirming the independent distribution of the two carnivores.

Table 3 Comparison of co-occurrence models for red fox, stone marten and badger, based on camera trapping. Only models with $\Delta AIC_c \leq 2$ are shown.

Model	-2logL	K	AIC_c	ΔAIC_c	AIC_c wt
Red fox and stone marten					
Ψ^{RF}, $\Psi^{SMRF} = \Psi^{SMrf}$, $p^{RF}(EUC) = r^{RF}(EUC)$, $p^{SM}(EUC) = r^{SMrf}(EUC)$, r^{SMRF}	1.00	7	940.32	0.00	0.53
Ψ^{RF}, $\Psi^{SMRF} = \Psi^{SMrf}$, $p^{RF}(EUC) = r^{RF}(EUC)$, $p^{SM}(EUC) = r^{SMrf}(EUC)$, $r^{SMRF}(EUC)$	0.90	8	940.54	0.22	0.47
Badger and stone marten					
Ψ^{B}, $\Psi^{BSM} = \Psi^{SMb}$, $p^{B}(EUC) = r^{b}(EUC)$, $p^{SM}(EUC) = r^{SMb}(EUC)$, $r^{SMB}(EUC)$	1.00	8	672.89	0.00	0.81
Badger and red fox					
Ψ^{B}, $\Psi^{RFB} = \Psi^{RFb}$, $p^{B}(EUC) = p^{RF}(EUC) = r^{B}(EUC)$, $r^{BRF}(EUC)$, $r^{Brf}(EUC)$	1.00	8	850.01	0.00	0.36
Ψ^{B}, $\Psi^{RFB} = \Psi^{RFb}$, $p^{B}(EUC) = r^{B}(EUC)$, $p^{RF}(EUC)$, $r^{RFB}(.)$, $r^{RFb}(EUC)$	0.42	9	851.75	1.74	0.15
Ψ^{B}, $\Psi^{RFB} = \Psi^{RFb}$, $p^{B}(EUC) = r^{B}(EUC)$, $p^{RF}(EUC) = r^{RFB}(EUC) = r^{RFb}(EUC)$	0.40	6	851.85	1.85	0.14

-2log L: 2log-likelihood; K: number of parameters; AIC_c: Akaike's Information Criterion; ΔAIC_c: delta AIC_c; AIC_c wt: AIC_c weight. Ψ = probability of occupancy. p = probability of detecting a species given absence of the other species from the site. r = probability of detecting a species given both species are present (capital letter) and/or present but undetected (lower case letter) r was also estimated as a function of eucalypt.

RF – red fox; SM – stone marten; B – badger; EUC – eucalypt plantations

The detectability of stone marten varied in the same way as described for the red fox. The lowest value was reached when both badger and stone marten were present and detected, in eucalypt plantations ($p^{SMB(Euc)}$ =0.00±0.00), increasing slightly in areas with different land cover (p^{SMB}=0.07±0.05). The non-detection or absence of badger increased stone marten detectability, even in eucalypt areas ($p^{SM(Euc)}$ = $r^{SMb(Euc)}$ = 0.22±0.03).

Again, there was no influence of badger on red fox occupancy (ψ^{RFB}=ψ^{RFb}=0.95±0.04) (Table 3). The red fox detectability reached its lowest value, in eucalypt plantations, when badger was absent ($p^{RF(Euc)}$=0.10±0.03) (Table 3; Fig. 6). The presence and detection of badger increased red fox detectability, in both areas without eucalypt (r^{RFB}=0.68±0.08) and with eucalypt ($r^{RFB(Euc)}$=0.63±0.09). When the badger was present, but not detected, red fox detectability decreased slightly ($r^{RFb(Euc)}$=0.51±0.04). The two best explanatory models presented an average φ of 1.07 ± 0.06, slightly above zero, indicating that these two carnivores were distributed independently of one another.

Temporal partitioning

In general, the activity patterns of the three species confirmed intensive nocturnal and crepuscular movements, with activity peaks around 23:00 and 04:00 (Fig. 7). No temporal segregation was observed amongst the three carnivores and the coefficient of overlapping of daily activity patterns was very similar in areas dominated by eucalypt stands (Site A) and areas dominated by evergreen oak and montados (Site B), for the 24 hour period and for the activity period (between 18:00 and 6:00). For the 24 hour period, the coefficients ranged from 0.77, in Site B, between red fox and stone marten and badger and red fox, to 0.87, in Site A, between red fox and stone marten (Fig. 7). For the activity period, the coefficients ranged between 0.75, in site B, between red fox and stone marten, to 0.85, in Site A, between stone marten and badger.

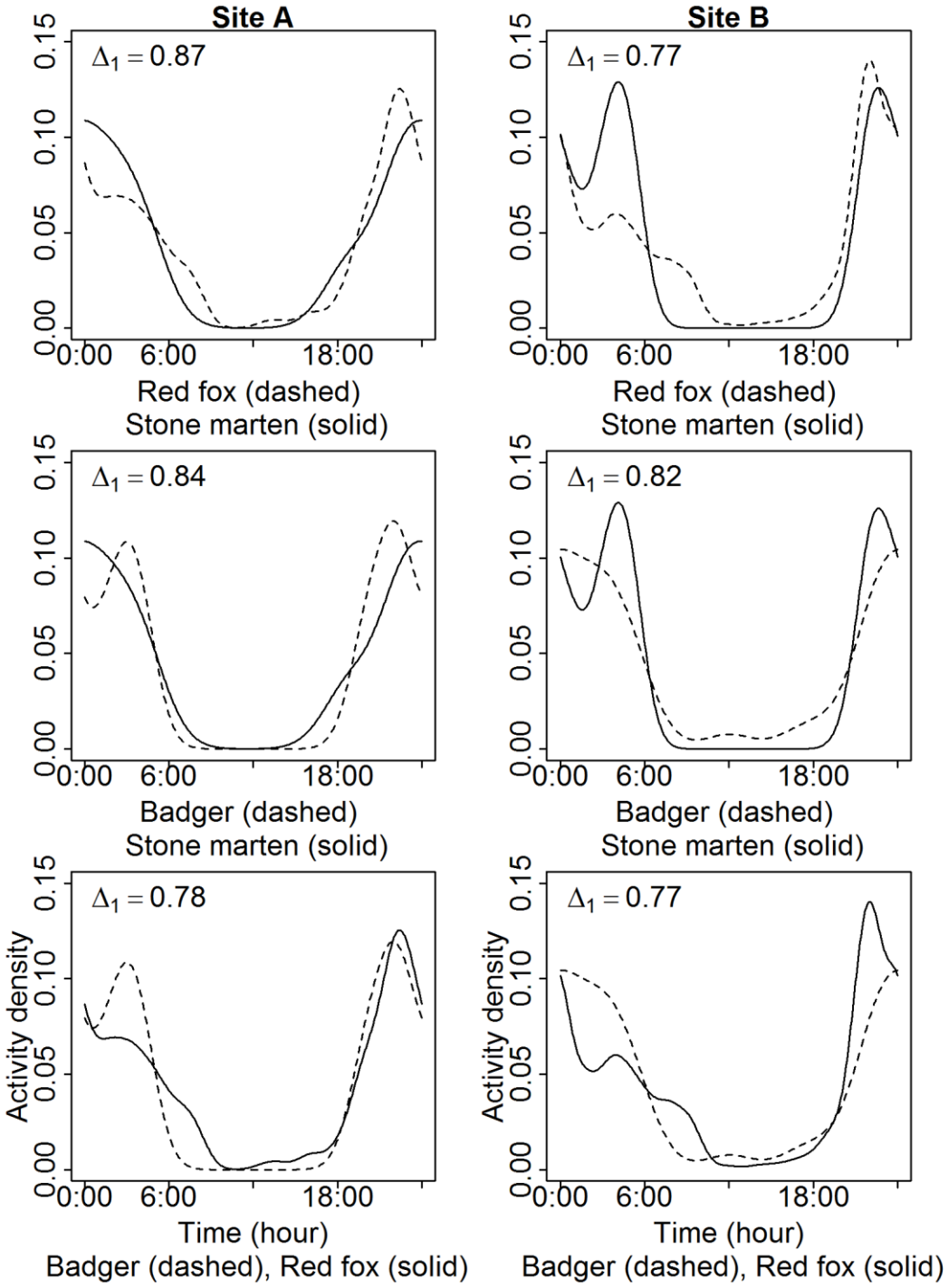

Fig. 7 Coefficient of overlapping of daily activity patterns between the red fox, *Vulpes vulpes*, and the stone marten, *Martes foina*, the badger, *Meles meles*, and the stone marten and the badger and red fox in Site A, with the main land cover being eucalypt plantations, and in Site B, dominated by evergreen oak forests and *montados*

Discussion

Eight main points stand out from our results, some of which support our initial hypotheses:

1. For all species, detection probability decreased with the extent of eucalypt area in both single and co-occurrence models;
2. Badger displayed a preference for a patchy and diverse landscape;
3. Eucalypt had a negative influence on the occupancy of red fox, and red fox and stone marten displayed a preference for evergreen oak forest;
4. Stone marten detection probability decreased slightly in the presence of badger or red fox.

However, some of our results were contrary to expectations:

5. In co-occurrence models, the occupancy values were similar between eucalypt plantations and *montados*;
6. No temporal segregation was observed between the different species and there were no significant differences in activity patterns between or within *montado* and eucalypt plantations;
7. Red fox was not influenced by badger in terms of either occupancy or detection probability;
8. Stone marten occupancy was not affected by either red fox or badger.

The dynamic balance that allows intraguild species to coexist in the same landscape can be disrupted by disturbances according to their intensity and extent, and their effects on species interactions (Lindenmayer and Fischer 2006). Some authors confirm the avoidance of eucalypt areas by red fox, stone marten and badger (Revilla et al. 2000; Rosalino et al. 2004; Pereira et al. 2012), whereas others support the preference of red fox and badger for this open forest (Santos and Beier 2008; Pita et al. 2009), highlighting the need for a complex understorey layer to support shelter and prey. In accordance with their known plasticity (Macdonald and Sillero-Zubiri 2004), red fox chose a mix of close (evergreen oak forests) and open (open farmland) habitats, whereas stone marten preferred evergreen oak forests as described in previous studies (Virgós and García 2002; Spinozzi et al. 2012). Oak forests have a

complex vegetation structure, with high diversity and multidimensional structure, often associated with a high number of food resources, such as fruits (Rosalino et al. 2010a) and birds, that comprise part of the stone marten's diet, leading to greater numbers of predators. This complexity may influence interspecific interactions among carnivores in different ways. Complexity may lead to exclusion or reduction of subordinate predators either through direct competition or because more complex habitats make it more difficult for intermediate competitors to detect the top predator (Thompson and Gese 2007). However, our results do not support this premise, since in our study area, both stone marten and red fox used oak forests, questioning the hypothesis of habitat partitioning. The predation of marten, a similar mustelid to stone marten, by red fox is common (Lindström et al. 1995), so the probable overlap of diet and habitat may increase the opportunity for intraguild predation. However, carnivores with arboreal behaviour, such as stone marten, may be favoured by the vertical use of complex habitats, resulting in some resource partitioning but at a micro-scale. This may also decrease the level of competition, giving access to food resources as well as further shelter to this species that is not available to the red fox (Janssen et al. 2007; Hunter and Caro 2008; Pereira et al. 2012).

Carnivore diet in the Mediterranean region is diverse, with a high diet overlap amongst mesocarnivores i.e. a preference of fruits, small mammals, and birds, with seasonal or local specialisations [red fox: see review in Díaz-Ruiz et al. (2013); stone marten: Barrientos and Virgós (2006); Santos et al. (2007): badger: Rosalino et al. (2005a)]. The badger is not as well adapted to this seasonality in prey availability as red fox and stone marten (Virgós and Casanovas 1999b), and it showed the lowest occupancy values along with the highest variability (standard error). The badger is a generalist feeder (Rosalino et al. 2005a), but when it has to shift its diet from earthworms, its main food resource in North of Europe, in favour of fruit, mammals and invertebrates in the Mediterranean region, its distribution becomes more restricted and density declines (Virgós and Casanovas 1999b; Rosalino et al. 2004). The study area is very dry, and although we did not monitor earthworms, those habitats are not rich in this prey (Virgós and Casanovas 1999b). The preference shown by the badger for a patchy landscape, with a high number and diversity of patches, might therefore be associated with a larger number of prey opportunities and

shelter (Virgós and Casanovas 1999a; Rosalino et al. 2010b), a process that Rosalino et al. (2004) refer to as habitat complementation.

Temporal activity is another niche axis, which in our research showed a high degree of overlap, with no time segregation detected and no influence of land cover. Red fox presented some crepuscular activity, both at dawn and dusk, but otherwise nocturnal activity was common across our three species as stated in previous studies (Rosalino et al. 2005b; López-Martín et al. 2008). The risk of an interspecific aggressive encounter may be increased in: (1) low-quality habitats such as eucalypt plantations where it would be expected that the foraging time would be higher, increasing the rate encounter; and (2) good quality habitats, preferred by the carnivores, such as oak forests, which may lead to distinct temporal use in order to avoid agonistic meetings (Carothers and Jaksić 1984). Since eucalypt plantations were avoided by carnivores and the preferred habitats are complex and allow for vertical use, no interference competition related to temporal activity was observed.

The lack of any detectable effect of interspecific competition on occupancy is contradictory to some studies (badger-red fox: Macdonald et al. (2004); Trewby et al. (2008); red fox-marten: Lindström et al. (1995)). Nevertheless, recent work by Barrull et al. (in press) referred to a significant overlap of space and activity pattern during summer, when food availability is high. Our results may be explained by this or by the possibility that the scale of the study may not have the fine resolution to assess spatial-temporal avoidance. The presence of a dominant species might force the subordinate to relocate even if it is for a limited time. For example, stone marten could move a short distance for a brief period to avoid red fox and badger, as is found in other species e.g. coyote and kit fox (White et al. 1995). Indeed, the detectability of stone marten decreased slightly with the presence of the other carnivores. On the other hand, the presence of badger increased the detection of red fox, which is difficult to explain given the reported dominance of the badger over the fox (Macdonald et al. 2004). However, this positive association may be because red foxes associate badgers with good foraging sites and follow them to those resources (Macdonald et al. 2004).

The most significant effect of eucalypt plantations on this carnivore community was to decrease detectability across all three species. In open farmlands or oak forests, cameras were often placed on trails, which are very evident in these habitats, increasing the probability of an encounter. However, eucalypt plantations, with their open, simple and homogeneous structure are very difficult for finding trails when they exist, decreasing the probability of detection. The occupancy models we used take into account the probability of detection and correct the probability of occupancy, so this would not have biased our results (Gibson 2011). Nevertheless, when detections probabilities are <0.15, such as for the badger and stone marten in 2011, it is difficult to distinguish sites where the species is truly absent from ones with low detection probability and the model estimates requires careful analysis (MacKenzie et al. 2002; Bailey et al. 2004). Our findings highlight that habitat preferences have a greater impact on detectability and occupancy for these carnivores than interspecific competition, with a strongly negative effect of eucalypt plantations on occupancy across all three species. However, they also highlight the importance of using models that can correct for differences in detectability for inferring interspecific competition, especially when species occur at low densities.

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Supplementary Information

Table S1 Description and summary of the explanatory variables used to examine the influence of landscape on the carnivore occupancy, determined on a 1 km radius around each camera

Variable (unit)	Code	Description	Transformation
Landscape Cover (%)		% of each land cover	
Eucalypt	EUC		Angular
Oak Forest	OakFor		Angular
Oak Montado	OakMon		Angular
Olive	Ol		Angular
Open Farmland	OpenFarm		Angular
River	Riv		Angular
Rock	Rock		Angular
Scrub	Scrub		Angular
Landscape structure			
Patch area mean (ha)	AREA	The mean area of all the patches	Logarithmic
Largest Patch Index (%)	LPI	The percentage of the landscape comprised by the largest patch, measures the dominance	
Edge density (m/ha)	ED	Length of edge structures per hectare	Logarithmic
Euclidean Nearest-Neighbour distance (m)	ENN	The shortest straight-line between two patches of the same land cover	Logarithmic
Proximity index	PI	Evaluates the mean patches isolation, the closer to 0 the index, the more the patches are isolated from each other	Logarithmic

Table S1 Cont.

Variable (unit)	Code	Description	Transformation
Interspersion and Juxtaposition index (%)	IJI	Quantifies the landscape configuration and considers the proximity of all patches. This index quantifies which patch types are interspersed, with the highest value (IJI = 100) occurring when the corresponding patch type is equally adjacent to all other patch types	Angular
Landscape shape index	LSI	Measures the perimeter-to-area ratio A more complex shape will have a higher ratio than a less complex shape.	Logarithmic
Number of patches	NP	Number of patches in the landscape	
Patch Richness	PR	Number of patches	
Shannon's Diversity Index	SHDI	Measure of relative patch diversity	
Shannon's Evenness index	SHEI	Measure of patch distribution and abundance	

CHAPTER 5

DISCUSSION

5.1 Summary

In Chapter 1, I discussed the expansion of forest plantations over the last two decades. I also highlighted the impact on biodiversity of forest plantations and of particular silvicultural practices and the problems caused by a preference for the use of exotic species such as the eucalypt. Overall, natural forests harbour higher biodiversity than forest plantations, and plantations of native species have greater species richness than exotic plantations. Nevertheless, plantations may favour generalist, open habitat and pioneer species in certain situations, especially when primary forest has a dense canopy with reduced light reaching the undergrowth. I also described the importance of forest plantations in rehabilitating degraded land. I further considered the drivers of biodiversity in the Mediterranean basin as an important biodiversity hotspot and the threats within the region and to the native habitat *montado* (habitat destruction and alteration, land abandonment and introduction of exotic species). I underlined the extension of the eucalypt afforestations especially in the Mediterranean region and the paucity of research published so far on the impact of these exotic plantations on biodiversity in that area. Finally, I described in general terms the focal groups I had chosen in order to evaluate the impact of exotic plantations – amphibians, bats and carnivores.

In Chapter 2, I assessed the influence of the landscape and local variables on amphibian presence in 88 ponds distributed in *montados* and eucalypt plantations, considering three spatial scales – local (pond), intermediate (400 m buffer), and broad (1 km buffer) scales individually and in combined scale models. I sampled the ponds using a combination of dipnetting, visual surveys and acoustic night surveys. Thirteen species were detected during the survey, the most common being *Pelophylax perezi*, *Hyla arborea/meridionalis*, *Lissotriton boscai*, *Pleurodeles waltl* and *Triturus marmoratus*, which were present in more than half of the ponds. I used a generalised linear mixed model, with a binomial error distribution (to model species occurrence) and a Poisson error distribution (to model species richness). Models with a combination of environmental covariates of the different spatial scales

had stronger support than those taken individually. Invasive fish presence, a local variable, was the most important variable for most of the species occurrence models, with the exception of *P. cultripes* and *H. arborea/meridionalis*. Eucalypt plantations had a negative impact on the occurrence of the newt *L. boscai*, but not on the remaining species. Eucalypt plantations had the opposite effect on *S. salamandra,* whose presence was favoured by this exotic stand. Therefore, the expected negative impact of these exotic plantations on the amphibian community was not confirmed, unlike the negative impact of exotic fish. I suggested that forest managers should prevent new fish introductions and eradicate fish from already occupied ponds when possible.

In Chapter 3, I compared the overall bat activity and species richness and focussed on Kuhl's bat *Pipistrellus kuhlii* (the most abundant bat species in the area) activity between eucalypt plantations and native *montado* habitat using a bat detector. I examined the influence of stand, landscape and survey variables within plantations on the response variables. I used generalised linear mixed models with a zero inflated Poisson distribution to model the results. Hawking and generalist bats of the genus *Pipistrellus* were the most frequently detected species. Bat activity, species richness and *Pipistrellus kuhlii* activity were higher in native *montado* than in any of the eucalypt stands. Nonetheless, mature eucalypt plantations showed the highest bat activity and species richness, while clear-cut areas showed the lowest. Generally, within individual eucalypt stands, the response variables were positively associated with low-level understorey and high-level tree clutter, tree height and night temperature, but negatively associated with distance to the nearest water point. The results suggested that in order to promote bat diversity and activity in exotic eucalypt plantations in the Mediterranean region, it is important to: (1) provide a high density of water points; (2) maintain plots of mature plantations; and (3) promote understorey clutter.

In Chapter 4, I tested the impact of eucalypt plantations on niche partitioning in a carnivore community consisting of red fox (*Vulpes vulpes*), badger (*Meles meles*) and stone marten (*Martes foina*). Based on data from camera trapping, I evaluated the influence of eucalypt plantations on species occupancy and detection in single-species and co-occurrence models and on temporal activity. Eucalypt cover

negatively influenced detection probability across all species in both single and co-occurrence models. Eucalypt plantations had a negative effect on occupancy of red fox, which preferred open farmland and evergreen oak forest. Stone marten preferred large patches of oak forest while badger occupancy was positively influenced by patch richness. Occupancy of any one species was not influenced by the presence of any other species. Despite having an effect on the detection and occupancy of all three carnivores, eucalypt plantations had no effect on the interactions within this carnivore community.

5.2 Eucalypt plantations: impact on biodiversity

The results gathered in this study have made an important contribution to the understanding of the impact of eucalypt plantations on biodiversity. The study has demonstrated that it is overly simplistic to tag eucalypt plantations as "ecological deserts" (Gardner et al., 2007), and the impacts vary for different taxonomic and functional groups. Eucalypt plantations have a negative impact on carnivore occupancy, because although no influence in the co-occurrence interactions was found, red fox, stone marten and badger all preferred native, patchy habitats over eucalypt plantations. Bat activity was also lower in eucalypt plantations than in native *montados*, although species richness was very similar in native and mature eucalypt forests. Only amphibian occurrence seemed to be generally unaffected by eucalypt plantations, with the exception of two species, with opposing results (*L. boscai* negatively and *S. salamandra* positively).

5.3 Forest management practices to promote biodiversity

Characteristics of eucalypt stands and landscape were also evaluated to assess which variables would impact species richness and occurrence in order to infer management guidelines to enhance biodiversity. The results highlight the exclusion/removal of exotic fish and conservation of permanent ponds for amphibians, the importance of ponds and understorey vegetation for bats and the maintenance of native and patchy habitats for carnivores.

Ponds and fish exclusion

Construction of ponds is a management action welcomed by foresters, especially in an area with a high fire risk like the Mediterranean region (Tedim et al., 2013) because suits both biodiversity (Seibold et al., 2013) and wildfire fighting (Blanchard & Ryan, 2007). A network of both temporary and permanent ponds to assure exotic fish free ponds together with water all year around, within amphibian dispersal distance, e.g. 1 km apart, is a management action that can easily be incorporated cost effectively into forest projects, with positive consequences for other faunal groups (Céréghino et al., 2010; Hassall et al., 2011; Seibold et al., 2013).

Some permanent ponds are managed by angling associations for sports fishing, without any aim of economic profit, in spite of the recreational and well-being benefits of the activity (FAO, 2012; Hickley & Tompkins, 1998). Although not directly related with silviculture practices, considering the impact of exotic fish on biodiversity but also the benefits of angling, I would recommend eradicating exotic fish from already occupied ponds, whenever possible. Where this action is not possible, assuring a network of temporary ponds, as mentioned above, would make it difficult for fish to thrive (Ferreira & Beja, 2013; Jakob et al., 2003; Montori, 1997).

Promotion of understorey vegetation

Another forest management practice that it is recommended according to the results presented in this research is the promotion of understorey vegetation, which has a positive impact for most of biodiversity (Carnus et al., 2006; Simonetti et al., 2013; Zou et al., 2014). However, it is a management measure that may encounter some opposition by foresters. Mega-fires in the Mediterranean have become more frequent over the past decade (Tedim et al., 2013), the promotion of understorey vegetation can increase fire risk (Mitchell et al., 2009) and it is expected that with predicted climate change, these events will become more common (Pawson et al., 2013).

Promotion of diverse age stand plantations

Clear-cut plots can affect biodiversity, reducing species richness and abundance, difficulting migration and dispersion (Hartley, 2002; Homyack et al., 2011; Popescu et al., 2012). Nevertheless, open-habitat species can be favoured by this new habitat, such as the black-eared wheatear (*Oenanthe hispanica*) or the corn bunting (*Miliaria*

calandra) (Vallecillo et al., 2013). Mature stands favour forest species which prefer more complex structured habitats, like most forest bats. The maintenance of plots of different age stands is recommended to promote a diverse landscape that suits the different requirements of both open and forest-species (Hartley, 2002).

Promotion of patchy landscape

One of the drivers of the biodiversity on the Mediterranean region is the patchy, mosaic landscape, with multiple and dynamic land uses and land covers (Blondel, 2006). It was discussed in Chapter 1 how land abandonment and afforestations leading to homogeneous landscapes are threatening biodiversity (Pienkowski et al., 1998). The results presented in Chapter 4 support the recommendation of maintaining and promoting patchy landscape with native habitats, which were preferred by the carnivores studied. The typical mosaic landscape has a complex vegetation structure, associated with high number of prey opportunities and shelter (Rosalino et al., 2010; Virgós & Casanovas, 1999).

Two possible management approaches could be taken to conciliate biodiversity and eucalypt plantations. The first approach is a complex forestry plantation (Lindenmayer et al., 2003), which focuses on multiple uses, integrating a multiplicity of functions, such as timber, biodiversity, recreation, and carbon fixation (Koch & Skovsgaard, 1999). Stand heterogeneity and complexity should comprise stand structure and age but also different patch sizes and shapes (Lindenmayer et al., 2000). In this approach, for instance, plots of plantations with understorey vegetation would be scattered across the landscape, mainly on north-facing slopes, to decrease the fire risk (Araújo, 1995).

The second approach which incorporates functional zoning is known as the triad approach (Seymour & Hunter, 1992). As the name suggests, it divides the landscape into three zones according to their main function: conservation, ecosystem-based management and intensive management. The aim of this approach is the implementation of these three functions as a whole in the landscape and not promotion of exclusion zones. This second approach would (1) avoid monocultures across large areas; (2) preserve patches of species-rich forests to act as sources to colonise nearby areas (Martín-Queller et al., 2013); (3) improve connectivity,

adapted for each species or group of species and at each spatial scale (Lindenmayer & Cunningham, 2013); (4) expand the range of uses and opportunities to adapt to possible stochastic changes (McNeely, 1994); and (5) also accommodate complexity and heterogeneity in plantations by having a range of age stands of different patch sizes and shapes (Lindenmayer et al., 2000). Seymour and Hunter (1992) described the triad approach to be implemented in a forested landscape. Nevertheless, it can be adapted to the Mediterranean mosaic landscape with a large number of dynamics land uses and land covers. The triad approach, at a landscape scale, and the complex forestry plantation approach, at the plantation scale, can be complementary, promoting biodiversity and a multiple use landscape.

5.4 Eucalypt plantations, biodiversity and silvicultural practices – needs for future research

Although my results are limited geographically, which implies a particular response to present physiographic and edapho-climatic conditions, past land uses and surrounding landscape, they highlight the potential impacts of eucalypt plantations on biodiversity and the use of management practices to minimise them. Even though this research relied on species occupancy, species richness, carnivore interactions and bat activity, a deeper study is needed to address more groups and in different parts of the Iberian Peninsula, where eucalypt plantations are predominant. Because the impact of eucalypt plantations is different among taxonomic groups and among species, it is recommended a multi-species study, using a hierarchical approach, at both local and landscape scale. It should cover the impact on soil properties and different taxonomic groups as well as the possible effects of eucalypt plantations on population dynamics, body condition, and functional connectivity, which could make a significant contribution to enhancing our understanding of how to enhance sustainability in exotic plantations. Most plantations in the region are over 30 years old, it would be important for both present, and potential future planted areas to be assessed in relation to their long-term effect on plant communities. The need to assess silvicultural practices such as maximum size of clear-cut areas and size of areas without fuel management are just two examples that can impact connectivity and fragmentation that have been overlooked in the region.

As a final remark, considering the high importance of eucalypt plantation products have in Portuguese export markets, it is recommended that parallel to the assessment of any change of management practice to promote biodiversity should also be an evaluation of its cost and its impact on yield.

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